VALIDATING A GPS COLLAR-BASED METHOD TO ESTIMATE PARTURITION EVENTS AND CALVING LOCATIONS FOR TWO BARREN-GROUND CARIBOU HERDS

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Abstract

In remote landscapes, it is difficult and expensive to document animal behaviors such as location and timing of parturition. When aerial surveys cannot be conducted as a result of weather, personnel or fiscal constraints, analyses of GPS collar movement data may provide an alternate way to estimate parturition rates and calving ground locations. I validated two methods (population-based method and individual-based method), developed to detect calving events of sedentary woodland caribou, on multiple years of data for two different migratory barren-ground caribou herds in Alaska, the Porcupine and Fortymile herds. I compared model estimates of population parturition rates, individual calving events, calving locations and calving dates to estimates from aerial survey data for both herds. For the Porcupine herd we also compared model estimates of annual calving ground sizes and locations of concentrated calving area centroids to those found with aerial survey. More years of data would be required for additional statistical power but for both the Porcupine and Fortymile herds, we found no significant difference between the population-based and individual-based method in: 1) individual classification rate accuracy (0.85 vs. 0.88, respectively; t = -7, P = 0.09, df = 1 and 0.85 vs. 0.83, respectively; t = 0.46, P = 0.69, df = 2) or 2) annual average distance from aerial survey calving locations (8.9 vs. 7.8 km, respectively; t = 0.16, P = 0.90, and 5.2 vs. 3.7 km, respectively; t = 1.03, P = 0.20). Median date of calving was estimated within 0-3 days of that estimated by aerial survey for both methods. Population parturition rate estimates from aerial survey, the population-based and individual-based methods were not significantly different for the PCH or FCH (0.91, 0.88 and 0.95, respectively; F = 0.67, P = 0.60, df = 2, and 0.83, 0.83 and 0.96, respectively; F = 3.85, P = 0.12, df = 2). Ultimately, more years of data would be required to support or reject the lack of significant differences between methods that we observed.

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General Introduction

Life history events such as survival, reproduction, and migration are often driven by movement (Hemming 1971, Bowyer et al. 1999, Morales et al. 2010). With the advent of global positioning system (GPS) transmitters, biologists are now able to monitor fine-scale movements of animals that are logistically difficult to access, such as those in remote areas (Bowman et al. 2000, Cagnacci et al. 2010, Hebblewhite and Haydon 2010, Urbano et al. 2010). The GPS technology allows non-invasive observation of migration routes, non-migratory movements, habitat use and other location-specific attributes (Rempel et al. 1995, Skupien et al. 2016). Because GPS transmitters record fine-scale movements they have facilitated analysis of wide-ranging phenomena such as predation rates and prey composition (Knopff et al. 2010) and diving behavior of marine mammals (Kuhn et al. 2010). In ungulate species such as moose, elk, and woodland and barren-ground caribou, GPS data have been used to estimate calving dates from movement rate declines, turning angles, and minimum convex polygon analyses (Dzialak et al. 2011, Nagy 2011, DeMars et al. 2013, Mcculley et al. 2017, Cameron et al. 2018, Nicholson et al. 2019).

Barren-ground caribou (*Rangifer tarandus granti*) are a gregarious species that have a life history dependent on movement (Fancy et al. 1989). The species migrates seasonally from wintering grounds to spring/summer grounds, where calving occurs in a relatively short pulse which may swamp predators and reduce individual predation risk for calves (Hamilton 1971, Hemming 1971). Both the Porcupine caribou herd (PCH) and the Fortymile caribou herd (FCH) exhibit these seasonal migrations to varying degrees (Valkenburg and Davis 1986, Griffith et al. 2002). The current method for monitoring population parturition rate (proportion of females that have calved) and individual calving locations for both herds is aerial surveys. However, these

surveys are often hampered by weather conditions, access to fuel, and distribution of caribou across the landscape. With the PCH facing potential oil development within their calving grounds, and the FCH exhibiting large population size fluctuations, it will continue to be important for managers to monitor parturition as one of several indicators of herd reproductive status (Boertje and Gardner 2000, Griffith et al. 2002).

DeMars et al. (2013) developed and validated two methods to estimate population parturition rates and individual parturition classifications for woodland caribou (*Rangifer tarandus caribou*) based on GPS-collared adult female movement rates. Both methods analyze female movement rates during the calving period and assume that a decline in movement is an indicator of calving (DeMars et al. 2013). DeMars et al. (2013) contended that potential dependence in travel rates among females of migratory caribou might make their methods inappropriate for migratory caribou. Migratory individuals travel *en masse* and when they reach the calving ground, they slow down, regardless of reproductive status, and non-parturient animals may be misclassified as parturient, as observed from satellite collared animals (Brad Griffith, personal communication). Despite this concern, DeMars's method has been applied to migratory barren-ground (Cameron et al. 2018) and migratory woodland caribou (Bonar et al. 2018) with some degree of success. Bonar et al. (2018) based their analyses on 2-hr GPS fix rates and one year of validation data while Cameron et al. (2018) used coarse fix rates (8-hr), sparse aerial survey validation data, and presented the combined percent agreement across six years between aerial survey and the DeMars et al. (2013) methods.

This study differed from other applications as I had fine scale GPS collar data (2.5-hr fix rates), and I had multiple years of validation data for two different migratory caribou herds with notable differences in annual movement rates (~5,000 km/y (PCH) and ~2,700 km/y (FCH)).

The goals of the study were to compare model output from DeMars et al.'s (2013) individual-based (IBM) and population-based (PBM) models to aerial survey validation data in terms of: population parturition rate, accuracy in individual parturition classifications and differences in location and timing of individual calving events for both the PCH (Chapter 1) and FCH (Chapter 2). For the PCH only, I also compared model and aerial survey output in terms of annual calving ground overlap and location of concentrated calving areas.

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Chapter 1: Porcupine Caribou Herd – Validating a GPS-based method for estimating parturition events and calving locations[1]

1.1 Abstract

Analysis of caribou movement patterns allows biologists and wildlife managers to better understand life history strategies such as location and timing of parturition. DeMars et al. (2013) developed methods to detect parturition events of woodland caribou based on a decline in movement rates from GPS collars. A previous study of barren-ground caribou adapted the DeMars methods and estimated agreement between aerial survey and model results to be 0.77-0.81 (Cameron et al. 2018). However, the DeMars methods have not been applied to a barren-ground herd that has fine-scale temporal data (GPS locations every 2.5 h vs. every 8 h) which may allow for more accurate identification of calving events. Additionally, the ability of the DeMars et al. (2013) models to predict annual calving grounds (ACG) and individual calving site locations has not been evaluated. In this study, we adapted the DeMars statistical methodologies, the population-based method (PBM) and the individual-based method (IBM), for the Porcupine caribou herd (PCH) for two years, to compare model estimates of population parturition rates, individual calving events, calving locations and dates, annual calving ground overlap, and location of concentrated calving area (CCA) centroids to those obtained from aerial survey data. Across-year population parturition rate averaged 0.91 (aerial survey, 0.98 and 0.84 for 2017 and 2018, respectively hereafter), 0.88 (PBM, 0.91 and 0.84) and 0.95 (IBM, 0.93 and 0.96) while individual classification accuracy averaged 0.85 (PBM, 0.93 and 0.76) and 0.88 (IBM, 0.96 and 0.80). Distance between aerial survey calving locations and those estimated by PBM and IBM

[1] Hepler, J., B. Griffith, J. Falke, J. Roach, J. Caikoski and M. Cameron. Porcupine caribou herd – Validating a GPS-based method for estimating parturition events and calving locations. Manuscript in preparation for *The Journal of Wildlife Management.*

were 8.9 km (3.24 and 14.62 km) and 7.8 km, respectively (9.16 and 6.43 km). Distance between CCA centroids derived from aerial survey and PBM or IBM averaged 11.2 km (4.6 and 17.9 km) and 1.7 km (2.3 and 1.2 km), respectively. PBM estimates of the ACGs (99% fixed kernel) had 91% and 92% overlap while IBM estimates had 95% and 94% overlap with aerial survey estimates. The median calving date predicted from the PBM was on the same day (5/31/2017) or one day before (6/1/2018) the median dates estimated by aerial survey data. The median calving date predicted from the IBM was one day later (6/1/2017 and 6/3/2018) than the dates estimated by the aerial survey data. Likely due to variability within and between the 2 years and limited statistical power we found no supporting evidence for a difference among model and aerial survey estimates of parturition rate ($F = 0.67$, $P = 0.60$, df = 2) or a difference between IBM and PBM accuracy in individual parturition classifications ($t = -7$, $P = 0.09$, df = 1). Additionally, we found no difference between the PBM and the IBM in the distance of modeled concentrated calving area centroids from those derived from aerial surveys ($t = 1.32$, $P = 0.41$, df = 1) or in the average distance of modeled calving locations from aerial survey locations ($t = -0.06$, $P = 0.95$, df = 1). Ultimately, more years of data would be required to support or reject the lack of significant differences between methods that we observed.

1.2 Introduction

Ungulate parturition rates and calving locations can be important indicators of future population health (body condition, population size and survival rates), particularly when human development may restrict access to habitats (Gunn et al. 2008, Dzialak et al. 2011, Taillon et al. 2012, Johnson and Russell 2014). Parturient barren-ground caribou (those that are pregnant or have recently calved) are more sensitive than non-parturient females and males to disturbances from development of infrastructure and associated activities in the Arctic (Smith and Cameron 1983, Dau and Cameron 1986, Cameron et al. 1992). Forecasted oil development in the 1002 Area of the Arctic National Wildlife Refuge (ANWR), therefore, may displace the Porcupine Caribou Herd's (PCH) concentrated calving areas (CCA) as females calve elsewhere to avoid infrastructure (Murphy and Curatolo 1987, Cameron et al. 1992, Griffith et al. 2002). The CCA is of high significance for population growth, likely dampening a decline and facilitating future recovery as calves born within the CCA have a 11 % higher probability of survival than those born in the periphery of the annual calving grounds (ACG) where calving density is lower and predation risk may be higher (Griffith et al. 2002). Additionally, calves born within the 1002 Area also have a higher survival rate (8%) than elsewhere due to available foraging resources and increased distance from the foothills where predation risk may be higher (Griffith et al. 2002). If the PCH relocates calving to avoid human activity, calf survival could decrease, reducing population size in the future (Fancy and Whitten 1991, Griffith et al. 2002).

Aerial survey is the traditional method used to identify calving locations and subsequently to delineate CCAs and ACGs (Whitten 1995, Griffith et al. 2002). However, many factors limit the feasibility of aerial surveys. For example, unsafe weather-related flying conditions precluded or limited completeness of surveys for years 2013-2015 for the PCH

(Alaska Department of Fish and Game, personal communication). Other factors include pilot/observer availability and location of fuel caches in relation to the distribution of the herd. Additionally, calving dates and locations estimated from the surveys may be inaccurate due to movement of females after they calve (Griffith et al. 2002). For example, a calf and cow pair may move 2.5 km/d shortly after calving (Griffith et al. 2002). Therefore, the actual event of calving could have taken place within a 2.5 km radius of the recorded location if daily surveys are conducted. To avoid these limitations of aerial surveys, we evaluated established methods (DeMars et al. 2013) to predict parturition status and additionally estimate calving dates and locations using movement rates based on global positioning system (GPS) collar locations.

Radio-telemetry technology has greatly expanded biologists' ability to monitor animal behavior, habitat use, and survival (Gibson et al. 2013, Massé and Côté 2013, Rasiulis et al. 2014). Very high frequency (VHF) collars, an early telemetric method, required researchers to be relatively close to the animal to receive the radio signal that was emitted from the collar (Bowman et al. 2000). Getting close to an animal may not be possible depending on where the animal is located, weather, and landscape features (Bauduin et al. 2016). Over the past decade, GPS collars have gained increased application in wildlife management due to their ability to collect fine-scale movement data, avoid issues of inaccessible study areas and reduce the cost of data collection in the field (Bowman et al. 2000, Cagnacci et al. 2010, Hebblewhite and Haydon 2010, Urbano et al. 2010). GPS collars, which may operate year-round for multiple years, gather locations from the constellation of GPS satellites with accuracies ranging from 100 m to less than 10 m (Rempel et al. 1995). With GPS collar data, researchers can document migration routes, non-migratory movements, habitat use, and other location-specific attributes (Rempel et al. 1995, Skupien et al. 2016). By combining VHF and GPS collar technology researchers can

study more detailed behavioral events such as parturition (DeMars et al. 2013, Mcculley et al. 2017).

Intra-annual PCH movement rates have been documented with satellite- and GPS-collared caribou (e.g. Fancy et al. 1989, Griffith et al. 2002). For parturient females in the PCH, the lowest movement rates occur during the winter (November - April), with an increase in mid-April as the caribou return to their calving grounds (Griffith et al. 2002). After spring migration (end of May and early June), parturient females aggregate on the calving grounds and movement rates decrease to about 2.5 km/d at the time of calving (Griffith et al. 2002). This rate increases to 5 km/d within the week post calving as the calves are able to move at the same rate as adults (Griffith et al. 2002). In previous studies of large ungulates including moose and elk, a sustained decrease in movement rates during calving season has been interpreted as a calving event (Dzialak et al. 2011, Nagy 2011, DeMars et al. 2013, Mcculley et al. 2017, Nicholson et al. 2019).

DeMars et al. (2013) developed two models (hereafter: the DeMars method) to estimate calving events for woodland caribou from reduced movement rates of parturient females. Woodland caribou move much more slowly (<1 km/d) (Rettie and Messier 2001) than barren-ground caribou, such as the PCH (up to 20 km/d) (Griffith et al. 2002) during the post-calving and summer periods. As identified by DeMars et al. (2013) there is also a potential for a lack of independence among barren-ground caribou travel rates. Parturient woodland caribou move separately as individuals across the landscape to calve (DeMars et al. 2013). Conversely, parturient and non-parturient barren-ground caribou converge together on the calving ground and parturient animals calve within a short time frame in a pulse-calving event (Griffith et al. 2002). As both non-parturient and parturient females migrate to the coastal plain during calving season

(Fancy et al. 1989, Griffith et al. 2002), there is a possibility that they would both demonstrate a similar drop in movement rates once they reach the ACGs, creating potential dependence in movement rates between parturient and non-parturient females. This may cause the DeMars method to incorrectly identify non-parturient females as having a calving event, thus, over-estimating parturition rate. Despite these biological differences in woodland versus barren-ground caribou, the DeMars method was tested on the migratory Western Arctic barren-ground caribou herd (WAH) where calving events were predicted with 77-81% agreement with aerial surveys (Cameron et al. 2018). Cameron et al. (2018) noted that the lack of fine-scale temporal resolution in the GPS locations from the collars (8 h fix rate) and infrequent visual aerial observations likely reduced their accuracy estimates.

Although the PCH are migratory and woodland caribou are not, we hypothesized that the calving events of the PCH could be estimated from GPS-derived movement rates with similar accuracy as previous work (DeMars et al. 2013, Bonar et al. 2018, Cameron et al. 2018) with migratory and non-migratory woodland and migratory barren-ground caribou. The specific objectives of this project were to compare the following estimates obtained from the DeMars et al. (2013) individual-based method (IBM) and population-based method (PBM) to independent visual aerial survey estimates for barren-ground caribou of the PCH during 2017 and 2018: 1) population-level parturition rates and median calving dates; 2) the proportion of correctly classified parturient females (sensitivity), the proportion of correctly classified non-parturient females (specificity), the proportion of correctly classified females (accuracy) and estimates of individual calving locations; 3) the size and location of the ACGs and CCAs (Van Winkle 1975, Seaman et al. 1998, Griffith et al. 2002); and, 4) estimates of the potential displacement of CCAs from the eastern edge of the 1002 Area under a full development scenario.

1.3 Methods

Study Area

Our study focused on the annual calving grounds and concentrated calving areas of the PCH. The ACGs are primarily on the Arctic coastal plain in northeastern Alaska and in the Yukon Territory (Figure 1.1). The coastal plain is narrow (15-50 km) with low hills, lakes, ponds, rivers, and marshes (Monda et al. 1994). To the south is the Brooks Range, and to the north is the Beaufort Sea (Brown et al. 2016). The climate along the coastal plain is comprised of short cool summers (average July temperature 5°C) and long cold winters (average February temperature -20°C); snow and subfreezing temperatures can occur at any time of the year (University of Connecticut n.d., Monda et al. 1994). Coastal areas are typically snow-covered until June and annual precipitation is 10-30 cm (Johnson et al. 2007).

Study Population

The PCH was estimated at 218,000 individuals from a photocensus in July 2017 (Caikoski 2019, *in prep*). The PCH core annual range (derived from location data between 1982-2015) is approximately 201,000 km^2, encompassing northeastern Alaska in the United States, northern Yukon Territory (Yukon), and northwestern Northwest Territories in Canada (Hemming 1971, Fancy et al. 1989, Caikoski 2016) (Figure 1.1). Between November and April, the herd has overwintered in Alaska, to the south of the Brooks Range, and in the Richardson and Ogilvie Mountains in the Yukon (Griffith et al. 2002). Spring migration to the calving grounds along the Beaufort Sea begins in mid-April and continues through May and early June (Griffith et al. 2002). The PCH has shown variation in calving location, calving along the Alaskan coast in some years (1983-86, 1988-1991, 1998-99, 2002-03, 2005, 2010, and 2014-16)

and in Canada in other years (2000-01, 2004, 2006-07, 2009, and 2011-13) (Griffith et al. 2002, Pearce et al. 2018). In 1987, 1992, 1997, 2008 and 2014-15, calving was spread across both Alaska and Canada and delayed snow melt along the Alaskan coastal plain may be a factor that affects shifts in calving distribution (Griffith et al. 2002, Pearce et al. 2018). Following calving, the PCH begins migration back to their fall/wintering grounds in late June and early July (Griffith et al. 2002).

Aerial Surveys

We monitored 46 collared females ≥3 years old during the 2017 calving season and 50 collared females ≥3 years old during the 2018 season to estimate parturition status and calving locations. The collars were Lotek™ GPS collars, with auxiliary VHF transmitters that were placed on the caribou when they were ≥1 year old through a helicopter netgunning capture program implemented by Alaska Department of Fish and Game and Yukon Department of Environment personnel. The collars were programmed to collect a GPS location every 2.5 hours. We flew calving surveys in a fixed wing aircraft (Piper PA-18™ Super-Cub) from the end of May through early June with a pilot and an observer. GPS-collared females were located using VHF radio telemetry nominally every day, weather permitting, until a calf was observed and classified as parturient by the presence of 1 or 2 hard antlers and/or distended udder or a calf at heel (Whitten 1995). If a female was observed without at least one of the above characteristics or with new growth of soft (velvet) antlers, they were classified as non-parturient. Additionally, we estimated when and where parturient animals gave birth. If a calf was observed, the observer in the aircraft recorded coordinates with a handheld GPS unit. The first observation of a cow with a calf was assumed to be the calving date and location. For 2017, presence of a calf was confirmed with a second sighting on a subsequent day from the first sighting to ensure a calf had been

correctly identified. If there was a calf in the first observation, and none in the second observation, unless there was some question with the first sighting (such as a female was in a large group with multiple calves running next to her) the female was still classified parturient. For 2018, there was no second sighting confirmation due to poor flying conditions and reduced time available for surveys. Post-calving surveys were flown 2-3 weeks after initial calving surveys. If a female was seen with a calf in the post-calving survey and classified as non-parturient in the calving survey, her status was corrected to parturient and calving date and location were considered to be missing data.

Data Management

To prepare the data for application of both of the DeMars methods, the step length (straight line distance between consecutive GPS locations) between each 2.5 hour fix was calculated for every female. Every female's step lengths started with the same time stamp (5/26/2017 2:00 AM and 5/26/2018 2:00 AM) and followed the same 2.5 hour interval through the end of the calving window (June 30; 344 maximum total fixes) for both the PBM and IBM. If a female's GPS collar failed to obtain a location at a specific date/time, that location was given a null value as well as the subsequent location. For 2017, there were 40 missing fixes across females, 2018 had 45 missing fixes, and both years had an average of 343 fixes per female.

Population-based Method (PBM)

DeMars Approach

We initially attempted to use the cumulative distribution function (CDF) method described by DeMars et al. (2013) and a bootstrap method as implemented by Cameron et al. (2018) to identify a calving movement rate threshold. A movement rate (m/h) averaged over 3

days after calving was estimated from each female with a well-defined calving date. Females with well-defined calving dates were those that either had a clear and identifiable drop in GPS-derived movement rates, or a visual observation of a female without a calf on one day and with a calf the next day during the aerial survey (27 total females out of 46 for 2017, 12 total females out of 50 for 2018). We included all females with reliable visual calving observations regardless of movement rates and patterns or subsequent calf loss because we wanted a representation of movement at calving that took into consideration naturally fast or naturally slow moving females in the population. The beginning of the 3-day movement estimate started with the lowest observed movement rate either between the last survey observation without a calf and the first observation with a calf from aerial survey or from the lowest movement rate from the females with the clear drop in movement.

The distribution of 3-day average movement rates was smoothed by calculating a kernel density estimate (DeMars et al. 2013, Cameron et al. 2018). The smoothed distribution was then converted to a cumulative distribution function to represent the proportion of the population expected to move at or below a given rate. The 3-day average movement rate corresponding to the 98% quantile of the cumulative distribution was interpreted as the calving threshold. The 98% quantile removes the top 2% of the fastest movement rates and gives the proportion of individuals at or below the corresponding 3-day average movement rate. We used the 98% quantile as Cameron et al. (2018) found that the original 99.9% quantile proposed by DeMars et al. (2013) prevented the model from executing successfully. A possible explanation for this is that the Western Arctic herd (Cameron et al. 2018) had movement rates much higher than the woodland caribou studied by DeMars et al. (2013). Additionally, to account for variance in movement rates at calving that could influence the population calving threshold, we ran a 1,000-

iteration bootstrap (with replacement) that sampled 10 of the females with well-defined calving dates for each year (n = 27 and 12 for 2017 and 2018, respectively) and generated a calving threshold for each subset (Cameron et al. 2018). These estimates were combined into a histogram, a kernel density estimate was applied, and the maximum kernel estimate was used to identify the most common calving threshold movement rate (Figure 1.2).

We then compiled all adult (≥3-yr) female movement rates, parturient and barren, from May 26 to June 30 (46 females in 2017 and 49 females in 2018). This calving period was chosen because the earliest recorded calving event for the PCH was May 26th and no calving events have been recorded past June 30th (Griffith et al. 2002). We used a rolling 3-day average movement window to calculate an average movement rate for 3-day periods for every female during the calving period and compared this to the bootstrapped calving threshold rate. If a female's three-day average movement rate fell below the calving threshold rate, a calving event was declared. The calving event was defined as the date and time of the first GPS fix within the corresponding three-day average movement window that initially fell below the threshold (Figure 1.2A).

Modifications to DeMars Approach

While a 3-day average movement window yielded calving thresholds that correctly classified most parturient and non-parturient females for the woodland caribou (DeMars et al. 2013) and the migratory barren-ground WAH (Cameron et al. 2018), our preliminary analyses using 0.5, 1, 2, and 3-day average movement windows for both calving threshold estimation and parturition classification yielded very high calving thresholds (164 m/h – 528 m/h) for both 2017 and 2018 data, thus, over-estimating parturition events. Additionally, we obtained multimodal movement rate distributions for every combination attempted (Example: Figure 1.2) instead of the expected unimodal, normal distribution. Therefore, we visually reviewed plots of the

movement rates of all females for 2017 with a well-defined calving date and found that nearly all had travel rates that reached or dropped below 100 m/h for ≤ 1 day during our analysis period (26 May – 30 June).

Individual-based Method (IBM)

The IBM estimated two movement models for each female based on their individual rates: 1) a break in movement rate (the female did calve) and 2) no break in movement rate (the female did not calve) (DeMars et al. 2013). For the model of barren females, there is one scale parameter, interpreted as mean step length that is expected to remain constant during the analysis period, meaning there is no drop in movement rates to indicate a calving event during the analysis period. This mean step length was calculated for the entire analysis period (May 26–June 30) for all adult females. The model of calving females includes three parameters: 1) the mean step length, 2) the breakpoint in step length indicating calving, and 3) the time for the calf and cow to return to mean step length (DeMars et al. 2013, Appendix S3, ece3785-sup-0001-AppendixS1-S4.docx).

For the PCH, there were two sets of defined constraints used to run the models. The first set of constraints is the minimum number of steps before and after a calving event over which a movement rate must be averaged before a breakpoint can be identified. We defined this as 3 days (at 10 steps/d, 3 days = 30 steps). The other set of constraints was the minimum and maximum time for a cow/calf pair to return to mean movement rates, which we defined as 3 days and 15 days respectively (30 and 150 steps) based on observations of the WAH (Lent 1966). We did not attempt different values of the constraints because Cameron et al. (2018) found the IBM robust to changes in these values.

The IBM took each female's movement rate at each time step (2.5 hours) and applied both of the models (non-calving and calving). We used the lowest Akaike's Information Criterion (AIC) to identify the best fitting model, and subsequently whether or not a female had calved (DeMars et al. 2013). The calving event was characterized as the date and time of the GPS fix that occurred at the breakpoint of step length (Figure 1.3B).

Comparing the Annual Calving Grounds (ACGs) and Concentrated Calving Areas (CCAs)

To compare the ACGs and CCAs based on calving sites derived from the IBM and PBM methods to those derived from the aerial surveys, we first used the KernelHR program (Seaman et al. 1998) to analyze the estimated calving locations from each of the three methods. KernelHR uses fixed-kernel, Least Squares cross-validation specifications to create a utilization distribution, observation density, and raw kernel density estimates from the calving locations. Raw kernel density values for a grid encompassing all observations are reported at grid intersections. The utilization distribution is raw kernel density re-scaled to sum to a maximum value of 1.0 and estimates the probability of calving at various locations (Van Winkle 1975). The ACG is the 99% kernel contour of the utilization distribution, meaning 99% of calving was expected to occur within this boundary (Griffith et al. 2002). The observation density is the raw kernel density at each estimated calving site. The CCA is the contour on the raw density raster that includes greater than average observation density (Griffith et al. 2002).

We created polygons of the ACGs and CCAs from rasters of the utilization distribution, observation density and raw density KernelHR output using ArcGIS Desktop 10.5.1 (ESRI 2017). We overlaid the ACG and CCA polygons derived from the PBM and IBM estimates of calving locations on the aerial survey polygons individually to find the percent area overlap. We also found the distance between the centroids of the IBM and PBM CCA polygons from the

centroid of the aerial survey CCA polygons. If there was more than one CCA polygon, the centroid was derived from the largest polygon.

Additionally, we estimated the expected displacement of the CCAs derived from the two models and the aerial survey from the eastern boundary of the 1002 Area under a full development scenario using the methodology described in Griffith et al. (2002). The basis of this method is to maintain the shape of the CCA polygons, and shift them east and south, parallel to the Beaufort Sea, the minimum distance necessary to clear the boundary of the 1002 by 4 km (Griffith et al. 2002). This conservative baseline of displacement was considered appropriate based on observations of higher caribou density at least 4 km or more away from infrastructure (Cameron et al. 1992).

We also tested an alternative approach to delineating ACGs and CCAs using GPS data that relies on aerial surveys to identify parturition status but not calving sites. For this method, we took the location of all parturient females (classified from aerial surveys) on the long-term median calving date (LMC) (June 2) and created maps of the ACG and CCA to compare with the polygons created from aerial survey calving locations for each year with the methods described above. The median calving date is defined as the date when 50% of calving has occurred and the LMC (June 2) was calculated from 1983-2018 when aerial survey data were available (Griffith et al. 2002, Caikoski 2019).

Model Evaluation

For both models, estimates of individual parturition events and population parturition rates, calving locations, and calving dates were compared to those events, rates, locations, and dates estimated from the aerial surveys under the assumption that the aerial survey data

represented "truth". The R code (R Core Team 2015) for these models is detailed in DeMars et al. (2013), Appendices S1 and S3 (ece3785-sup-0001-AppendixS1-S4.docx), and edited by Cameron et al. (2018) in the supplementary materials (https://www.nrcresearchpress.com/doi/suppl/10.1139/cjz-2017-0314#.XaUFxkZKggw). We estimated sensitivity (proportion of correctly classified parturient females), specificity (proportion of correctly classified non-parturient females) and accuracy (proportion of correctly classified females). We calculated Cohen's kappa statistic (κ) (Cohen 1960) and the maximum attainable kappa (κ_{max}) (Sim and Wright 2005) to assess the magnitude of agreement between aerial survey and model estimates.

We conducted two-tailed paired t-tests ($\alpha = 0.05$) to test average across-year (2017 and 2018) between-model differences in: 1) the average distance between modeled and aerial survey estimates of individual calving site locations, 2) the differences in distance of modelled CCA centroids from aerial survey centroids, and 3) model accuracy. We tested for an average higher false positive rate across years (declaring a female parturient when she was not) compared to the corresponding false negative rate to address the DeMars et al. (2013) concern that their methods may not be appropriate for migratory caribou due to presumed dependence between parturient and non-parturient travel rates with a one-tailed paired t-test. We also conducted a two-factor (years and techniques) analysis of variance (ANOVA) without replication to test for differences among modeled and the aerial survey estimates of population parturition rate across years.

1.4 Results

Aerial Survey

In 2017, the weather conditions along the northern coast of Alaska and the Yukon were consistently conducive to flying as there was little wind, turbulence or fog. Additionally, there

was a relatively short (approximately 45 min – 1 h) commuting flight time from the airstrip to the herd. Of the 46 total females observed, 37 calving locations were recorded, 8 females were classified as parturient based on antler/udder status alone, and 1 was classified as barren. Back to back survey observations of a female without and with a calf on successive days were obtained for 13 of the 37 calving locations. The remaining 24 calving locations were recorded either on the first observation of a female, with no prior observations, or had multiple days in between survey observations without and with a calf. Of the 8 females classified as parturient based on antler/distended udder status alone and with no calving observation, 2 were seen with a calf on the post-calving survey. About 89% of the calving (33 out of 37) took place along the Alaskan coastal plain with only 11% of the calving locations (4 out of 37) in the Yukon. The average movement rate for all GPS-collared females in this study, during the analysis window (May 26-June 30) for 2017 was 504 m/h (95% CI = 482 – 527 m/h).

In 2018, weather conditions were highly variable, with wind blowing dense fog inland from the coast around midday, and dangerous turbulence in the foothills developed around the same time. Daily flight time to the herd also increased to around 2 h. This resulted in less time for daily observations of females. Of the 49 total females surveyed, only 25 calving locations were recorded, 16 females were classified as parturient based on antler/udder status alone, and 8 were classified as barren. Of the 25 calving locations, 13 were observed on consecutive days wherein the female was without, then with a calf. Additionally, 8 of the 16 females, classified as parturient based on antler/distended udder status alone and with no calf observation during the calving survey were later seen with a calf in the post-calving survey. About 48% of the calving (12 out of 25) took place on the Alaskan coast and 52% was in the foothills and river drainages of northern Yukon (13 out of 25). The average movement rate for all GPS-collared females in

this study, during the analysis window (May 26-June 30) for 2018 was 469 m/h (95% CI = 450 – 488 m/h).

Population-based Method Performance

We tested the 100 m/h calving threshold with average movements windows of 0.5, 1, 2 and 3-days and found that a 1-day movement window average correctly predicted the one non-parturient female and calving dates closest to those in the aerial survey in 2017. With an average movement window of 0.5 days, the movement rates had multiple declines below the calving threshold that gave early calving dates and classified non-parturient females as parturient. Any movement window higher than 1 day, smoothed the movement rates out so much that even known parturient females' movements did not decline below the threshold. For our analysis, we then used this 1-day average movement window with a 100 m/h calving threshold (1d/100m).

For 2017 data, the PBM estimated a parturition rate of 0.91 while the aerial survey estimated 0.98 (Table 1.1). With the 1-day average movement window and a 1d/100m calving threshold, 93% of females were correctly classified as parturient/non-parturient (n = 46) (Table 1.2 and 1.3). The PBM classified all but 3 parturient females as parturient, yielding high sensitivity (Table 1.2 and 1.3). One of these misclassified females was seen with a calf in the survey and about 5 hours after initial observation, she was observed again without her calf. The other two females were both classified as parturient based on presence of distended udders in the aerial survey but no calf was observed. Because there was a very low sample size of known non-parturient animals in the aerial survey (n = 1), the specificity was difficult to properly gauge; however, the PBM model correctly classified the only non-parturient female from the aerial survey correctly (Table 1.3). PBM median date of calving was the same day as the aerial survey estimate (5/31/2017) (range of 5/26 to 6/10) (Table 1.1). On average, the PBM estimated

individual calving dates on the same day (range -12 to 8 d) and 3.2 km (range 0.05-50.2 km) away from aerial survey locations (Figure 1.4A). An example of the PBM estimating an incorrect calving event compared to the aerial survey estimate can be found in Figure 1.5A.

In 2018, the PBM estimated the same parturition rate as the one estimated from the aerial survey (0.84) (Table 1.1). Accuracy was 0.76 (n = 49) (Table 1.2 and 1.3). The sensitivity was 0.85, classifying 35 of the 41 parturient females correctly (Table 1.2 and 1.3). While there was a much larger sample size of non-parturient females from aerial survey (n=8) than in 2017, the PBM had low specificity (0.25) because only 2 of those females were correctly classified (Table 1.2 and 1.3). The other 6 females that were incorrectly classified as parturient had estimated calving dates between June 5th and June 24th. On average, the PBM model identified calving dates 1.5 days earlier (range -12 to 2 days) (Table 1.1) and 14.6 km away (range 0.06 km to 170.2 km; if the outlier female distance of 170.2 km was removed, the average distance would only be 7.9 km rather than 14.6 km) (Figure 1.6A) from the calving date and location from the aerial survey. PBM median date of calving was 1 day earlier than the aerial survey estimate (6/1/2018 and 6/2/2018, respectively; range of 5/26 to 6/24) (Table 1.1).

On average across both years, the PBM had an accuracy of 0.84 and a suggestion of a slight (0.035) negative bias when estimating population parturition rates. However, estimated parturition rates were not significantly different among IBM, PBM, and aerial surveys ($F = 0.67$, $P = 0.60$, df = 2). Across years on average, the PBM estimated calving sites to be 8.9 km away (95% CI = 0 – 20.1 km) from, and 1 day earlier (95% CI = 2.5 days earlier – 0.5 days later) than those estimated by aerial survey. In addition, there was a notable, though non-significant difference between false positive and false negative rates for parturition classifications (0.38 and 0.11, respectively; $t = 0.801$, $P = 0.285$, df = 1) (Table 1.4).

Individual-based Method Performance

For 2017, the IBM predicted a population partition rate of 0.93 while aerial survey estimated 0.98. (Table 1.1). Accuracy and sensitivity of the IBM was high for 2017 (0.96 for both), only misclassifying two parturient females (Table 1.2 and 1.3). The IBM called the only non-parturient female correctly, resulting in the same specificity as the PBM for this year (Table 1.2 and 1.3). On average, the IBM predicted calving dates to be 1.5 days (range -2 to 11 days) later than aerial survey and 9.1 km (range 0.16 - 66km) away from survey locations (Figure 1.4B, Table 1.1). An example of the IBM incorrectly estimating a calving event can be found in Figure 1.5B. The median calving date estimated by the IBM model was one day later than the median estimated from the aerial survey (6/1/2017 and 5/31/2017, respectively; range of 5/26 to 6/17) (Table 1.1).

For 2018, the IBM predicted a population parturition rate of 0.96 while aerial survey estimated 0.84 (Table 1.1). IBM accuracy was 0.80 and sensitivity remained relatively high (0.95), only classifying 2 parturient females incorrectly (Table 1.2 and 1.3). However, the specificity of the model was 0 because it did not correctly classify any of the 8 non-parturient females (Table 1.2 and 1.3). On average, the IBM estimated calving dates 0.5 days later (range -5 to 12 days) and calving locations that were 6.4 km away from those estimated from aerial survey data (range 0.12 km to 65.44 km) (Figure 1.6B). The median calving date estimated by the IBM model was one day later than the median estimated from the aerial survey (6/3/2018 and 6/2/2018, respectively; range of 5/25 to 6/24) (Table 1.1).

On average across both years, the IBM had an accuracy of 0.88 and a suggestion of a slight (0.035) positive bias when estimating parturition rates. However, estimated parturition rates were not significantly different among IBM, PBM, and aerial surveys ($F = 0.67$, $P = 0.60$,

df = 2). Across years on average, the IBM estimated calving sites to be 7.8 km away (95% CI = 5.1 – 10.4 km) from, and 1 day later (95% CI = 0 days earlier – 2 days later) than those estimated by aerial survey. In addition, there was a notable, but non-significant difference between false positive and false negative rates for parturition classifications (0.5 and 0.05, respectively; t = 0.919, P = 0.264, df = 1) for IBM (Table 1.4).

Kappa and Maximum Attainable Kappa (κ_{max})

As an index of strength of agreement beyond that expected by chance, the magnitude of the kappa statistics for both the PBM and IBM suggested fair to moderate agreement in 2017 (0.38 and 0.48, respectively) and slight to poor agreement in 2018 (0.10 and -0.07, respectively) (range of values for Kappa can be ≤ 0 to 1) (Landis and Koch 1977). In addition, kappa values in 2017 were at the maximum values they could attain given the constraints of the marginal totals (κ_{max}) (Sim and Wright 2005) which was likely driven by the imbalance of known parturients and non-parturients in the dataset. However, the kappa statistic was not significantly different from zero for either model or either year indicating that neither model performed significantly better than chance (Table 1.2). There were no clear differences between PBM and IBM based on kappa and κ_{max} (Table 1.2).

Differences Between Models and Aerial Survey Across Years

There was no difference among PBM and IBM and aerial survey estimates of population parturition rate (0.88, 0.94 and 0.91, respectively; F = 0.67, P = 0.60, df = 2). Likewise, there was no average across year difference between the PBM and IBM in: 1) accuracy (0.85 and 0.88, respectively hereafter; t = -7, P = 0.09, df = 1), 2) estimates of false positive rates (incorrectly classified as parturient) (0.38 and 0.50; t = -1, P = 0.5, df = 1), 3) distance of model estimated

calving locations from aerial survey calving locations (8.9 and 7.8 km; $t = 0.16$, $P = 0.89$, df = 1) or 4) distance of model estimated CCA centroids from aerial survey CCA centroids (11.2 and 1.7 km; $t = 1.32$, $P = 0.41$, df = 1) across years.

Concentrated Calving Area and Annual Calving Ground Comparison

In 2017, the CCA and ACG derived from both the PBM and IBM tended to have a higher overlap with the CCA and ACG derived from aerial survey observations than the CCA and ACG based on GPS locations on the LMC date (Table 1.5). The IBM-derived CCA and ACG tended to have a higher percent area overlap with the aerial survey (82.4% and 95.3%, respectively) (Table 1.5) than the PBM-derived CCA and ACG (80.8% and 91.3%, respectively). The LMC CCA and ACG tended to have lowest percent area overlap with those derived from the aerial survey in 2017 but tended to have greater overlap with aerial survey polygons in 2018 (Table 1.5).

In 2018, the PBM, IBM, and LMC polygons tended to be larger than the corresponding polygons of the ACG and CCA from the aerial survey. The CCA and ACG polygons resulting from the PBM tended to have the lowest percent overlap with survey results of any of the methods (81.4% and 92.3%, respectively) (Table 1.5).

Across years, there was no significant difference between PBM and IBM models in the distance of respective CCA centroids from aerial survey CCA centroids (11.2 and 1.7 km, respectively; $t = 1.32$, $P = 0.41$, df = 1). However, in 2018, the displacement of the LMC centroid was in a different direction (N vs. W) than the PBM or IBM centroids compared to the aerial survey (Table 1.6).

Displacement of the Concentrated Calving Areas from the 1002 Area

For 2017, every concentrated calving area overlapped the 1002 Area and, thus, would be expected to have some displacement away from the 1002 Area given a full development scenario (Figure 1.7). The aerial survey, IBM, PBM, and LMC concentrated calving area polygons would have been displaced approximately 100 km to the southeast, to provide a buffer of 4 km from the eastern border of the 1002. For 2018, only the CCA from the aerial survey was within the boundary of the 1002 Area and its expected displacement as a result of full development was estimated to be 60 km (Figure 1.8).

1.5 Discussion

In this study, we compared predictions of two movement models (IBM and PBM; DeMars et al. 2013) to aerial survey estimates of calving locations and dates, sizes and locations of calving grounds, individual parturition events (sensitivity), individual non-parturient classifications (specificity), overall proportion of correctly classified adult females (accuracy) and population parturition rates for the migratory barren-ground Porcupine Caribou Herd for two years. Previous studies that evaluated the performance of the DeMars et al. (2013) methods (DeMars et al. 2013, Bonar et al. 2018 and Cameron et al 2018) have not addressed location accuracy and have not explicitly presented sensitivity or specificity estimates for adult female parturition classifications.

There are two classes of evaluations that are relevant to the assessment of DeMars et al. (2013) methods; 1) population level evaluations and 2) individual level evaluations. Population level evaluations include herd parturition rate, median calving date, and location of CCAs and ACGs. Individual level evaluations include accuracy, sensitivity and specificity and distance between aerial survey and PBM or IBM derived calving locations. Likely due to a small sample

size and large variability between years, we found no supporting evidence for differences among PBM, IBM, and aerial survey estimates of population parturition rate ($F = 0.67$, $P = 0.60$, df = 2). Additionally, we found no significant difference between distance of PBM and IBM modeled estimates of CCA centroid locations ($t = 1.32$, $P = 0.41$, df = 1), average distances of modelled calving locations ($t = 0.16$, $P = 0.90$, df = 1) compared to aerial survey locations, or accuracy in parturition classifications ($t = -7$, $P = 0.09$, df = 1).

Our estimated median calving dates from PBM and IBM were within one day of those obtained by aerial surveys (Table 1.1). Although not directly comparable to our work, Bonar et al. (2018) found substantial early bias in herd-wide parturition dates ranging from 1 week before the observed peak from hand-captured VHF collared calves (IBM) to 2 weeks before the observed peak from hand-captured VHF collared calves (PBM). Our agreement between aerial, PBM and IBM estimated calving date was likely enhanced by our concerted efforts to obtain daily aerial observations during calving. Infrequent aerial or ground based observations would be expected to result in later estimates of calving date than either PBM or IBM.

Our across-year estimates of accuracy for the migratory barren-ground PCH were 0.84 and 0.88 for PBM and IBM, respectively and these values did not differ significantly (t= -7, P=0.090, df = 1). Our estimates of accuracy fell between an upper level of $\geq$0.97 accuracy for PBM and IBM reported by DeMars et al. (2013) and 0.94 accuracy for PBM across migratory and sedentary herds reported by Bonar et al. (2018) and a lower level of 0.77 and 0.81 accuracy (PBM and IBM, respectively) reported by Cameron et al. (2018). Due to large among-year variability, our cross-year population parturition rates for the PCH did not significantly differ among aerial survey, PBM or IBM ($F = 0.67$, $P = 0.60$, df = 2).

For this study, we included all aerial survey parturition classifications when assessing performance of the DeMars et al. (2013) methods. Although some of these data may be less accurate than others (e.g., calving locations estimated from first observation of a female with a calf when she had no prior observations and calving locations obtained from observations with multiple days in between observations without and with a calf), we chose to retain all of the aerial survey observations. We did this to be consistent with the approach used by wildlife managers to estimate parturition rates in order to evaluate how well model output matched management indices traditionally derived from aerial surveys. We also used all aerial survey parturition classifications including those based on antler/distended udder status alone as well as females confirmed parturient with a calf at heel because these are the parturition classifications used by the Alaska Department of Fish and Game to estimate parturition rate. Additionally, we chose to evaluate both models separately in contrast to consensus approaches suggested by other studies (Bonar et al. 2018, Cameron et al. 2018). We did this to focus on the potential differences between models that require expensive validation data (PBM) and those that do not (IBM). Had we used a consensus approach, our accuracy estimates may have been higher but at the cost of reduced sample size.

All PBM and IBM derived centroids of CCAs tended to be west of aerial survey derived CCA centroids (Table 1.6) but there were no differences in distances between PBM and IBM centroids from aerial survey centroids ($t = 1.316$, $P=0.414$, $df = 1$). Distances of all three (PBM, IBM, LMC) CCA centroids from the aerial survey derived CCA centroids for both years were relatively negligible when considering the vast area of the extent of calving, 1982-2001 (Figure 1.1, Table 1.6). For 2017 (Figure 1.6), potential displacements of concentrated calving in response to full development of the 1002 Area (*sensu* Griffith et al. 2002) were quite similar

among aerial survey, PBM and IBM and LMC derived methods. In 2018, however, neither PBM, IBM nor LMC methods identified concentrated calving within the 1002 Area (Figure 1.7) and no displacement of the CCA as a result of full development (*sensu* Griffith et al. 2002) would have been predicted. Thus, GPS movement rate-derived estimates of concentrated calving areas may result in underestimates of the cost to calf survival of full development of the 1002 Area compared to aerial surveys. More years of validation data would be required to estimate whether this would be expected to be a regularly recurring or an occasional effect.

The 100 m/h calving threshold that we implemented for the PBM was much lower than any other threshold rate at calving noted for migratory barren-ground caribou (137 m/h and 208 m/h; Cameron et al. 2018, Bonar et al. 2018, respectively). However, previous work on the PCH found average parturient cow movements of 2.5 km/d at calving (Griffith et al. 2002). This is equivalent to about 104 m/h which coincides with our observation derived estimate of a 100 m/h calving movement threshold rate. Additionally, since our data was comprised of 2.5 h fixes, we expected that we would be able to detect such a low and often short-lived decline in movement rates. Although the visual method of estimating a calving threshold versus the bootstrapping threshold may be more time intensive, increase the chances of human error, and be unrepeatable if different observers conduct the visual estimation, it produced better accuracy for the PCH than the original CDF (DeMars et al. (2013) or Cameron et al. (2018) bootstrapping method. If the bootstrapping method for PBM does not perform well, we suggest visual inspection of movement rates during the calving analysis window to identify a potentially useful calving threshold. Then a sensitivity analysis of movement rates and average movement windows around this candidate movement rate can be conducted to choose the rate and average movement window that maximizes accuracy for PBM.

DeMars et al. (2013) proposed that migratory herds such the PCH may lack the independence among parturient and non-parturient female travel rates needed to accurately predict parturition because of aggregation behavior at calving. While the PCH is a migratory herd that moves as a group when migrating we found no evidence of a higher false positive rate compared to the false negative rate (PBM: 0.38 and 0.11 and IBM: 0.50 and 0.05, respectively; $t \leq 0.91$, $P \geq 0.264$, df = 1, one-tailed) that would be expected if dependence among parturient and non-parturient female travel rates had biased parturition rate estimates. Several anecdotal observations suggest that there is likely enough independence among individuals to detect non-parturient females versus parturient using GPS data. Typically the parturient females of the PCH lead the migration to the calving grounds and the non-parturient females and males lag behind (Lent 1966, Whitten et al. 1992, Caikoski 2011). Therefore, the likelihood of non-parturient females and parturient females reaching the calving ground at the same time and having the same movement rate during the pulse calving event may be reduced. There have also been observations of parturient females stopping to give birth while the rest of the group they were travelling with continued moving, thus exhibiting independence in movement rate from others (Lent 1966).

When executing the bootstrap method (Cameron et al. 2018) and creating the kernel density estimate of the movement rates for parturient females, we found a multi-modal distribution instead of the uni-modal distribution found by Cameron et al. (2018) (Example: Figure 1.2). This could mean that even within known parturient females, there are females moving at different speeds at calving that may require multiple calving thresholds for the PBM to accurately detect parturition events.

1.6 Management Implications

Location and timing of calving and parturition rate are all important indicators of habitat quality, forage availability, and forecasted health (body condition, population size and survival rates) of the population (Cameron et al. 1993, Griffith et al. 2002, Couturier et al. 2009). With proposed development of the 1002 Area in ANWR, there is a need for an alternative and reliable method to estimate calving metrics annually as aerial surveys may not be feasible, are costly, and may not reach peripheral members of the herd. Managers may consider several factors when deciding which DeMars method, if any, to use to predict parturition and calving events. For the PCH, of the two proposed movement rate-based models, the PBM required a novel approach to developing an effective calving threshold from known parturient animals as well as expensive validation data to develop this threshold. The IBM can be executed with the original code from DeMars et al. (2013) and did not require *a priori* information to run, but an estimate of the minimum and maximum number of days to return to pre-calving travel rates after calving was required and could be obtained from the literature. From our study, given no statistical difference between model output and aerial survey output, the decision of using either model may come down to the economics and ease of use of each model. The IBM model performed no worse than the PBM model in terms of accuracy, population parturition rate, calving locations and timing of calving and did not require expensive validation data.

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1.9 Figures

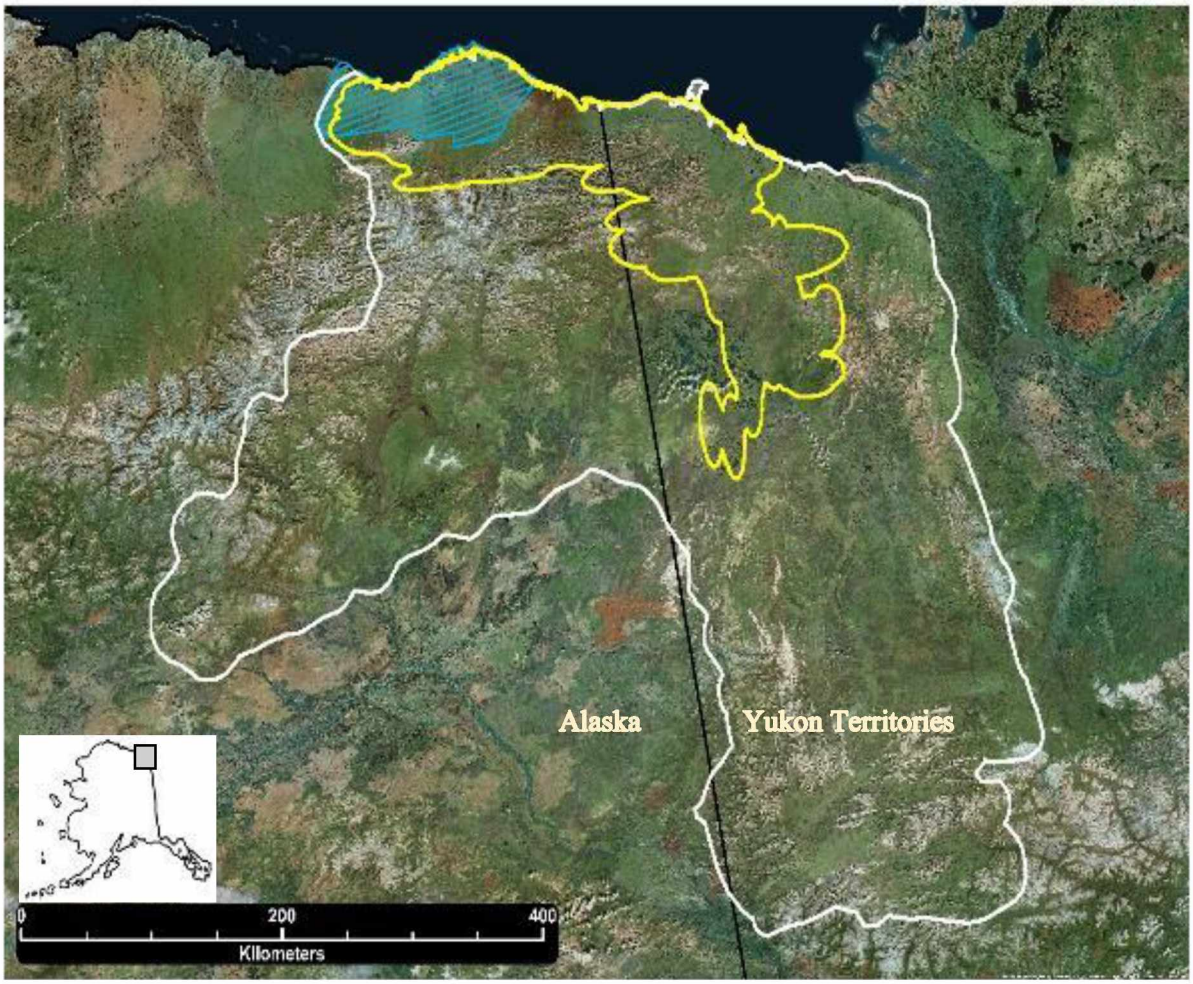

Figure 1.1: Porcupine herd annual range and extent of calving map. Core annual range of the Porcupine caribou herd (1982-2015, white line, (Alaska Department of Fish and Game 2016)), extent of calving (1982-2001, yellow line, outer perimeter of all annual calving grounds, (Griffith et al. 2002)), and the 1002 Area (blue striped area) in the Arctic National Wildlife Refuge.

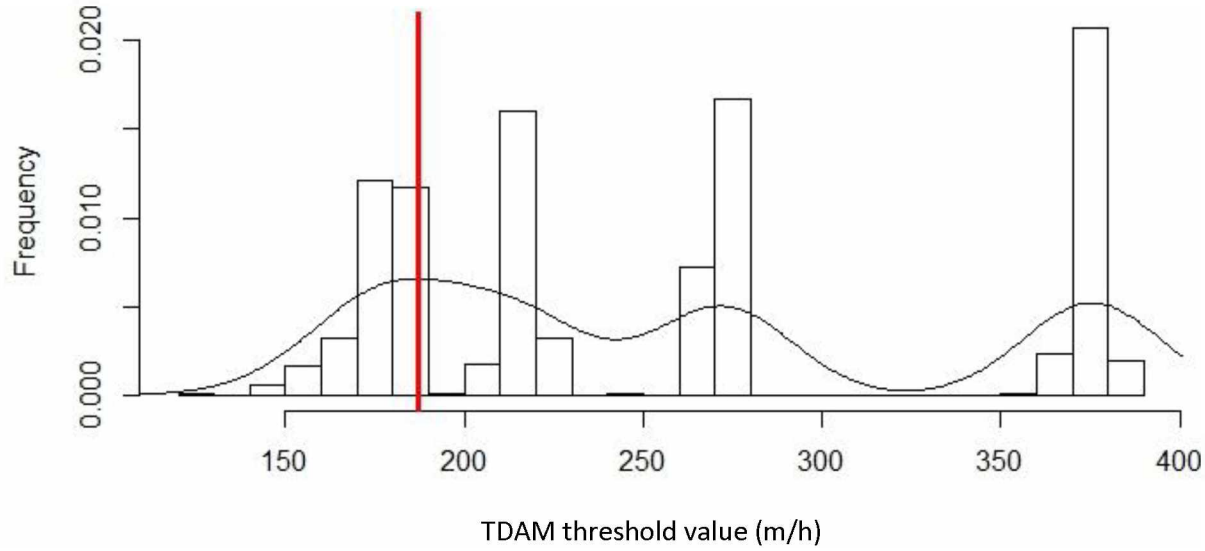

Figure 1.2: Calving threshold bootstrap histogram example. An example histogram showing the frequency of calving threshold 3-day average movement rates (TDAM)(m/h) found for females with a well-defined calving date from 2017 (n = 27) given from a 1,000-iteration bootstrap that sampled 10 individuals at a time (with replacement). A kernel density estimate was applied to the histogram and the maximum of the kernel density estimate (red line) (187 m/h) was the calving threshold movement rate (DeMars et al. 2013).

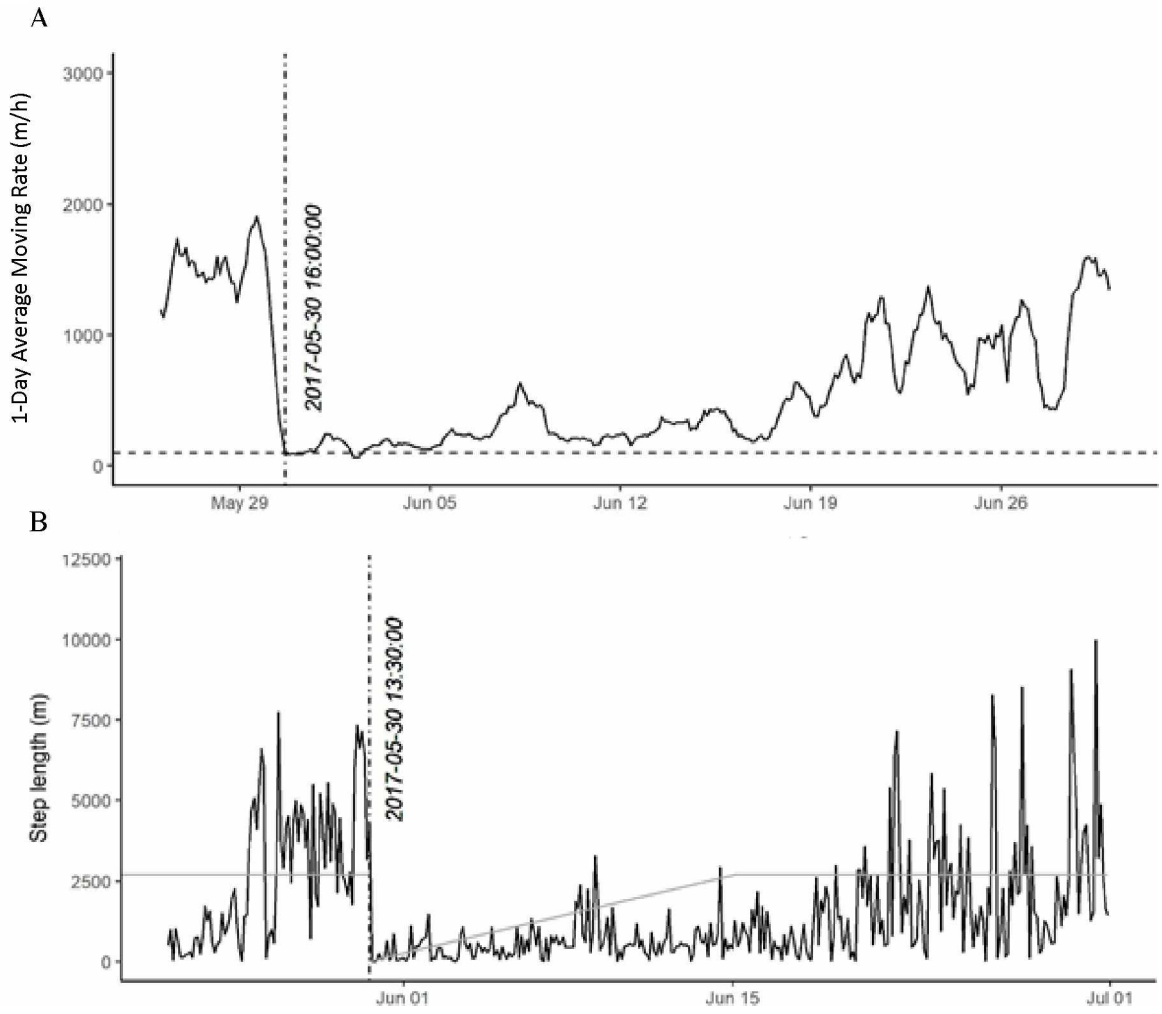

Figure 1.3: Model output of a calving date that matched the aerial survey. Parturition estimates for the same Porcupine caribou herd female for 2017 wherein model estimates of calving date matched the aerial survey. A) Population-based method output plot showing a calving date of May 30, 2017 with one-day average movement window and 100m/h calving threshold rate (1day/100m). B) Individual-based method output plot showing a calving date of May 30, 2017 with parameters set at 30 steps before and after a breakpoint, and a maximum and minimum of 150 and 30 steps, respectively for a cow/calf pair to return to average movement rates (30,150,30 as described in methods).

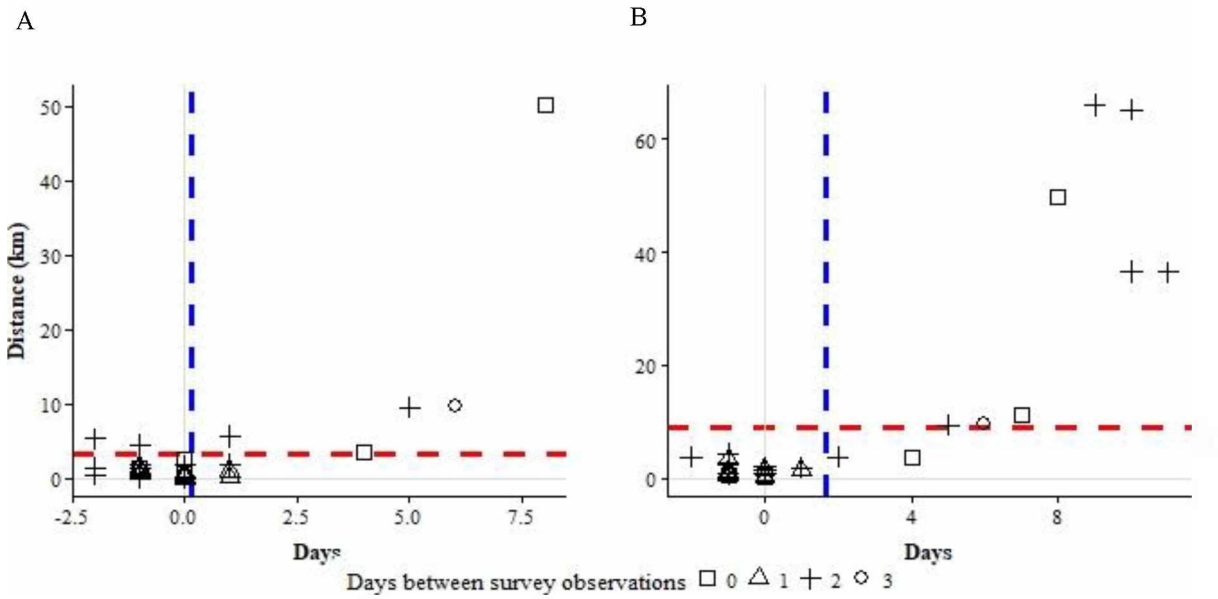

Figure 1.4: Distance and days between estimates of calving date and location for 2017. Distance and number of days between population-based method (PBM) or individual-based method (IBM) estimated calving sites and aerial survey estimates for the Porcupine caribou herd (PCH) for 2017. Along the y-axis is distance (km) from the calving sites observed in aerial surveys in 2017 (n = 36) to the calving site estimated by (A) PBM and (B) IBM, the red horizontal dashed line represents the average distance (3.24 km and 9.12 km respectively). Along the x-axis is the number of days before or after the aerial observed calving date in 2017 for the (A) PBM and (B) IBM estimated calving dates (negative implying earlier than the aerial survey observations, positive implying later than aerial survey observations). The blue vertical dashed line represents the average time difference for each model (0.17 and 1.67 days respectively).The shape of the symbols represents the number of days between observations during aerial surveys, 0 days means the first time the female was observed she had a calf at heel, 1 day means she was seen on initial observation without a calf and the following day with a calf, 2 days means she was seen the first day without a calf, there was no observation the second day, and she was seen with a calf on the third day, etc.

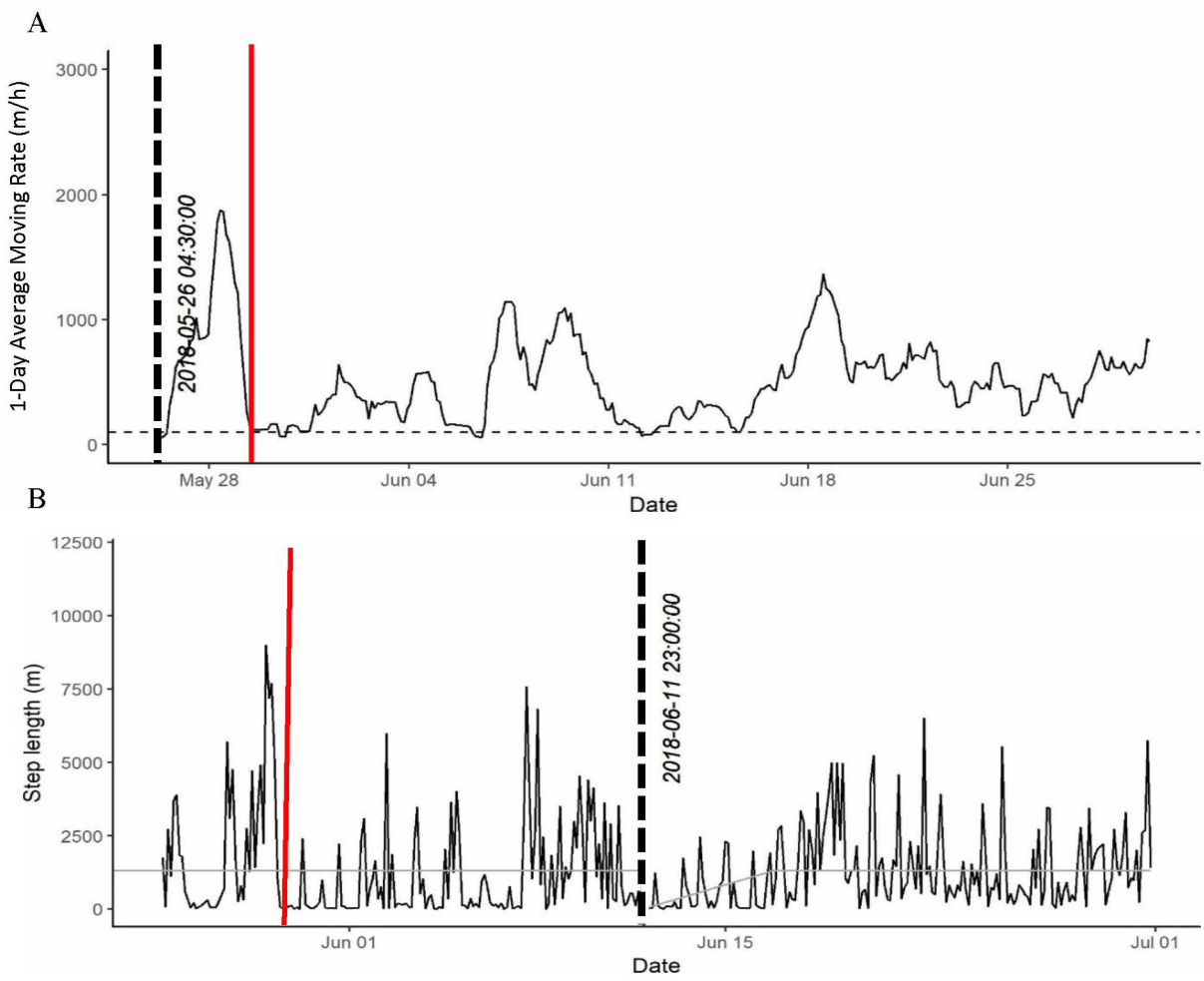

Figure 1.5: Model output of a calving date that did not match aerial survey. Parturition estimates for the same Porcupine caribou herd female for 2018. A) Population-based method output plot showing a calving date (black checked line) of May 26, 2018 with one-day average movement window and 100m/h calving threshold rate (1day100m). B) Individual-based method output plot showing a calving date of June 11, 2018 with parameters set at 30 steps before and after a breakpoint, and a max and min of 150 and 30 steps, respectively for a cow/calf pair to return to average movement rates. Red solid line in both panels shows the aerial survey calving date of May 30, 2018.

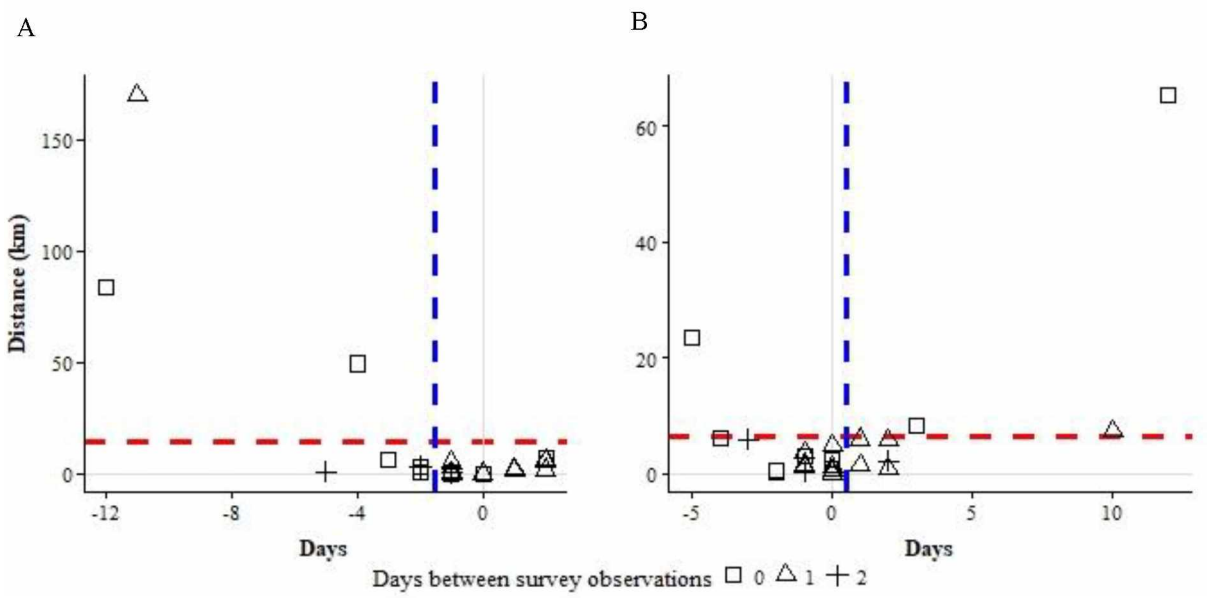

Figure 1.6: Distance and days between estimates of calving date and location for 2018. Distance and number of days between population-based method (PBM) or individual-based method (IBM) estimated calving sites and aerial survey estimates for the Porcupine caribou herd (PCH) for 2018. Along the y-axis is distance (km) from the calving sites observed in aerial surveys in 2018 (n = 24) to the calving site estimated by (A) PBM and (B) IBM, the red horizontal dashed line represents the average distance (14.62 km and 6.43 km respectively). Note the large scale difference on the y-axis for (A) the PBM, which is driven by one exceptionally large difference in distance of 170.2 km. Along the x-axis is the number of days before or after the aerial observed calving date in 2018 for the (A) PBM and (B) IBM estimated calving dates (negative implying earlier than the aerial survey observations, positive implying later than aerial survey observations). The blue vertical dashed line represents the average time difference for each model (-1.50 and 0.50 days respectively).The shape of the symbols represents the number of days between observations during aerial surveys, 0 days means the first time the female was observed she had a calf at heel, 1 day means she was seen on initial observation without a calf and the following day with a calf, 2 days means she was seen the first day without a calf, there was no observation the second day, and she was seen with a calf on the third day.

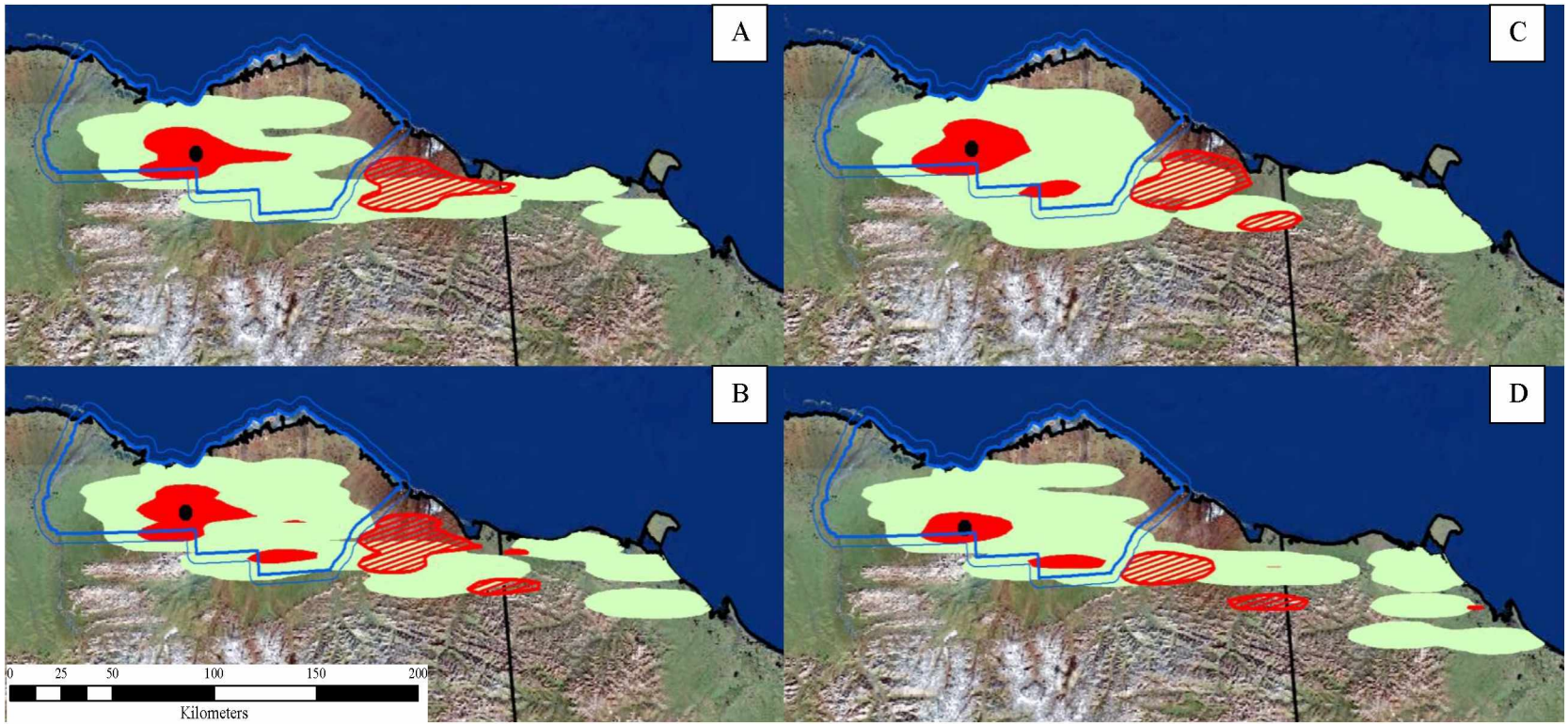

Figure 1.7: Maps of concentrated calving areas and annual calving grounds for 2017. Map of the concentrated calving area (solid red), annual calving ground (green), and centroid of the concentrated calving area (black dot) from Kernel HR output of A) aerial survey, B) population-based method (PBM), C) individual-based method (IBM), and D) long-term median calving (LMC) data for 2017. The 1002 Area border is delineated by the thick blue line and the thin blue line is the 4km buffer, which is the estimated minimum distance concentrated calving areas would be displaced from within the 1002 Area given full development. Expected displacement of the CCA to the southeast of the 1002 border is shown with red hashed polygons.

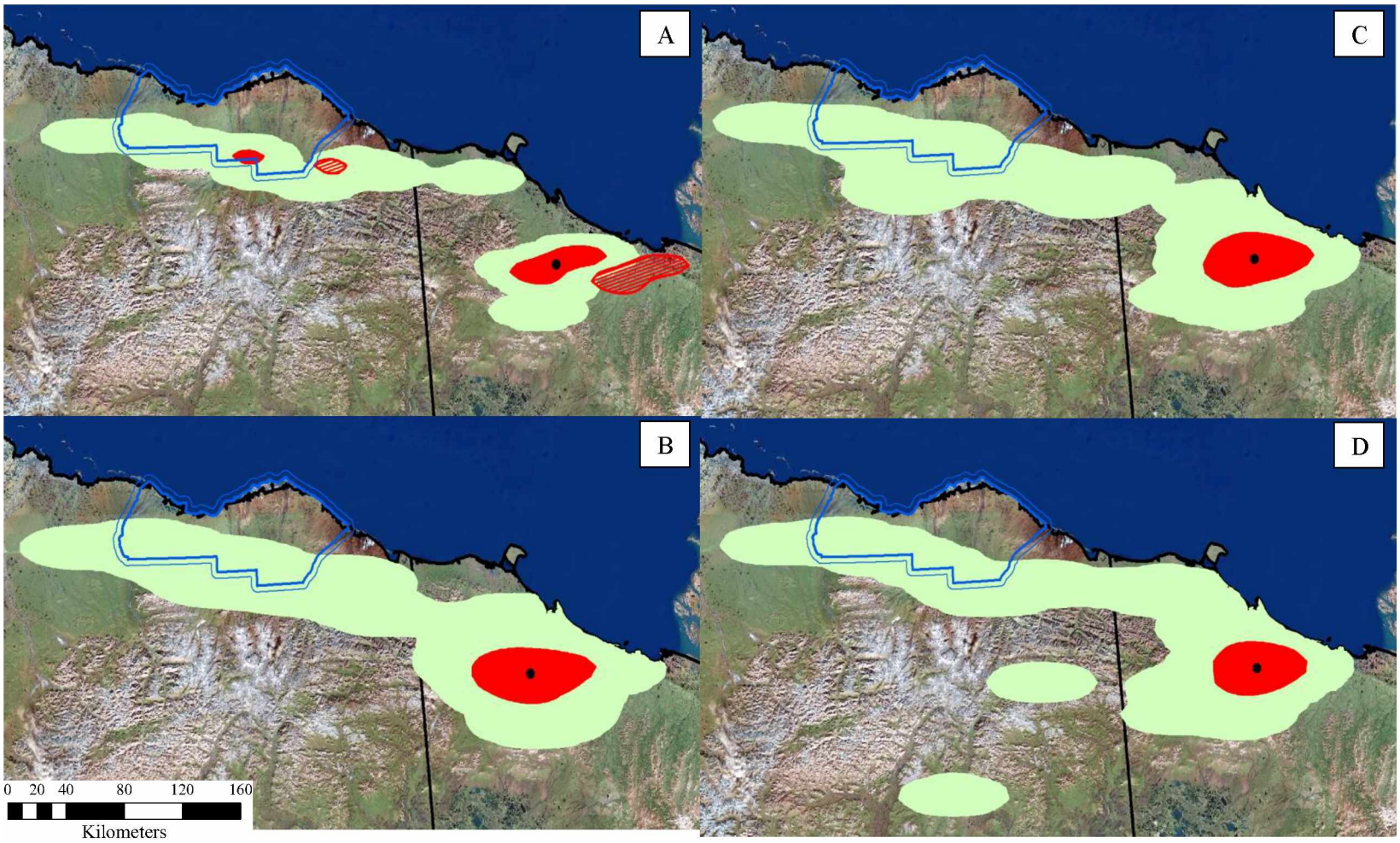

Figure 1.8: Maps of concentrated calving areas and annual calving grounds for 2018. Map of the concentrated calving area (solid red), annual calving ground (green), and centroid of the concentrated calving area (black dot) from Kernel HR output of A) aerial survey, B) population-based method (PBM), C) individual-based method (IBM), and D) long-term median calving (LMC) data for 2018. The 1002 Area border is delineated by the thick blue line and the thin blue line is the 4km buffer, which is the estimated minimum distance concentrated calving areas would be displaced from within the 1002 Area given full development. Expected displacement of the CCA to the east of the 1002 border is shown with red hashed polygons.

1.10 Tables

Table 1.1: Parturition rate and median calving date estimates. The parturition rate (percent of adult females that were parturient) and median calving date (date when 50% of calves have been born) estimated from population-based method (PBM) and individual-based method (IBM) compared to that estimated from the aerial survey for 2017 and 2018.

	Method	Parturition Rate	Median Calving Date
2017	Survey	98%	5/31/2017
	PBM	91%	5/31/2017
	IBM	93%	6/1/2017
2018	Survey	84%	6/2/2018
	PBM	84%	6/1/2018
	IBM	96%	6/3/2018
Average	Survey	91%	
	PBM	88%	
	IBM	95%	
Standard Deviation	Survey	10%	
	PBM	5%	
	IBM	2%	

Table 1.2: Sensitivity, specificity, accuracy, kappa, and κ_{max} estimates for both models. Measures of sensitivity (proportion of correctly classified parturient females), specificity (proportion of correctly classified non-parturient females), and accuracy (proportion of correctly classified females) of the population-based method (PBM) and individual-based method (IBM) in predicting parturition classifications of female caribou from aerial surveys. Additionally, the reported kappa (κ) statistic and maximum kappa (κ_{max}) found for each model with the 95% confidence intervals parenthetically listed below each kappa statistic is presented. The PBM was run at the 1day/100m calving threshold. The IBM was run with the parameters identified in the methods: 3 days allowed before and after a breakpoint, maximum time for calf/cow pair to return average movement rate of 15 days, and minimum time for calf-cow pair to return average movement rate of 3 days (step lengths: 30, 150, 30 respectively).

Performance Measure	Year	PBM	IBM
Sensitivity	2017 *(n=45)*	0.93	0.96
	2018 *(n=41)*	0.85	0.95
	Average	0.89	0.96
	Standard Deviation	0.06	0.01
Specificity	2017 *(n=1)*	1.00	1.00
	2018 *(n=8)*	0.25	0.00
	Average	0.63	0.50
	Standard Deviation	0.53	0.71
Accuracy	2017 *(n=46)*	0.93	0.96
	2018 *(n=49)*	0.76	0.80
	Average	0.85	0.88
	Standard Deviation	0.12	0.11
Kappa (κ)	2017	0.38 (-0.30 -1.06)	0.48 (-0.22 - 1.18)
	2018	0.10 (-0.34 -0.54)	-0.07 (-0.66 - 0.52)
κ_{max}	2017	0.34	0.48
	2018	1.00	0.36

Table 1.3: Confusion matrices from aerial survey data. Confusion matrices of the raw data collected from the 2017 and 2018 aerial surveys compared to the output of the population-based method (PBM) and individual-based method (IBM). 'Yes' means the female was classified as parturient. 'No' means the female was not classified as parturient.

2017

		Survey		
		Yes	No	Total
PBM	Yes	42	0	42
	No	3	1	4
	Total	45	1	46

		Survey		
		Yes	No	Total
IBM	Yes	43	0	43
	No	2	1	3
	Total	45	1	46

2018

		Survey		
		Yes	No	Total
PBM	Yes	35	6	41
	No	6	2	8
	Total	41	8	49

		Survey		
		Yes	No	Total
IBM	Yes	39	8	47
	No	2	0	2
	Total	41	8	49

Table 1.4: Proportion of false positives and false negatives for both methods. Proportion of false positive and false negative parturition classification from the population-based method (PBM) and the individual-based method (IBM) for the Porcupine caribou herd (PCH) and the average proportion and standard deviation of false positives and negatives across years and models.

	PBM		IBM	
	False Positives	False Negatives	False Positives	False Negatives
2017	0.00	0.07	0.00	0.04
2018	0.75	0.15	1.00	0.05
Average	0.38	0.11	0.50	0.05
Standard Deviation	0.53	0.06	0.71	0.01

Table 1.5: Area and overlap of concentrated calving areas and annual calving grounds. The total area, overlap area and percent area overlap of the concentrated calving area (CCA) and annual calving ground (ACG) for the population-based method (PBM), individual-based method (IBM), and long-term median calving date (LMC) method against the aerial survey method for 2017 and 2018.

		Method	Total Area (km^2)	Overlap Area (km^2)	Percent Overlap
2017	CCA	**Aerial Survey**	**816.92**		
		PBM	906.14	660.46	80.8%
		IBM	974.79	673.23	82.4%
		LMC	575.59	382.50	46.8%
	ACG	**Aerial Survey**	**7454.31**		
		PBM	7766.86	6805.73	91.3%
		IBM	9470.87	7106.14	95.3%
		LMC	8006.67	6504.34	87.3%
2018	CCA	**Aerial Survey**	**1067.07**		
		PBM	2301.20	868.13	81.4%
		IBM	1905.29	926.93	86.9%
		LMC	1746.62	915.31	85.8%
	ACG	**Aerial Survey**	**13703.56**		
		PBM	23849.70	12653.43	92.3%
		IBM	23431.80	12807.21	93.5%
		LMC	25055.04	13481.28	98.4%

Table 1.6: Distance and direction of concentrated calving area centroid displacement. The distance and direction of displacement of the concentrated calving area (CCA) centroids for the population-based method (PBM), individual-based method (IBM), and the long-term median calving date (LMC) method from the aerial survey CCA centroid for both years.

	2017		2018	
Method	**Distance (km)**	**Direction**	**Distance (km)**	**Direction**
PBM	4.55	282.2°	17.87	273.6°
IBM	2.27	274.5°	1.15	272.3°
LMC	5.92	232.8°	1.74	5.5°

Chapter 2: Fortymile Caribou Herd – Validating a GPS-based method for estimating parturition events and calving locations[2]

2.1 Abstract

Life-history strategies of barren-ground caribou can be better understood with analysis of movement patterns. DeMars et al. (2013) developed methods to detect parturition events of woodland caribou based on a decline in movement rates obtained from GPS collars. Previous studies of barren-ground caribou adapted the DeMars method to estimate agreement between model and aerial survey with 0.77-0.81 average accuracy (Cameron et al. 2018) and 0.84-0.88 average accuracy (Chapter 1). In this study, we adapted the DeMars et al. (2013) methodologies, the population-based method (PBM) and the individual-based method (IBM), for the Fortymile caribou herd (FCH) for 3 years to compare estimates of calving events and calving locations to aerial survey results. Among year (2016-2018, respectively, hereafter) population parturition rate averaged 0.83 (aerial survey: 0.82, 0.96, 0.72), 0.84 ((PBM: 0.74, 0.92, 0.83) and 0.96 (IBM: 0.90, 1.00, 0.98). Likely due to variability within and among the 3 years and limited statistical power we found no differences among PBM, IBM or aerial survey estimates of population parturition rate ($F = 3.85$, $P = 0.12$, df = 2). However, the 0.13 average difference, and consistent direction of differences across years, between IBM and aerial parturition rate suggests caution if using the IBM for FCH. Supporting this concern, the false positive classification rate was significantly greater than the corresponding false negative rate for IBM (0.90 vs. 0.02; $t = 10.14$, $P = 0.009$) supporting the DeMars et al. (2013) speculation that dependence in travel rates between parturient and non-parturient animals may negatively affect model performance. Across

[2] Hepler, J., B. Griffith, J. Falke, J. Roach, T. Bentzen and M. Cameron. Porcupine caribou herd – Validating a GPS-based method for estimating parturition events and calving locations. Manuscripts in preparation for *The Journal of Wildlife Management.*

the 3 years, individual classification accuracy averaged 0.85 (PBM: 0.86, 0.92, 076) and 0.83 (IBM: 0.80, 0.96, 0.74), and there was no statistical difference in these estimates ($t = 0.46$, $P = 0.69$). Average distances of model estimated calving locations from aerial survey calving locations were not significantly different between PBM and IBM (5.2 vs. 3.7 km, respectively; $t = 1.03$, $P = 0.41$, df = 2). The median calving dates estimated by the PBM were 1 to 3 days earlier than the aerial survey median dates. The median calving dates estimated by the IBM were within 1 day of aerial survey median calving dates. Ultimately, more years of data would be required to validate or reject the suspected IBM population parturition rate bias compared to aerial survey.

2.2 Introduction

Barren-ground caribou (*Rangifer tarandus granti*) (hereafter: caribou) have historically been an important resource for humans, with fossil records dating 12,000-15,000 years ago (COSEWIC 2016). Throughout history, caribou have been integrated into the socio-ecological background of indigenous cultures across Alaska and Canada as a source of food, culture, health and economy (Batal et al. 2005, Parlee et al. 2018). Today, caribou contribute to local economies as a source of subsistence food, as well as the larger economies through ecotourism and recreational hunting (COSEWIC 2016). In fact, caribou are the second most commonly hunted species in Alaska among residents and third for non-residents (ECONorthwest 2014). Although economically important, caribou populations have historically exhibited extreme fluctuations from highs in the hundreds of thousands, to lows numbering only a few thousand (Gunn et al. 2009, Vors and Boyce 2009). With climate warming in the Arctic and encroaching human development, caribou herds are facing a suite of challenges (Joly et al. 2011, Ernakovich et al. 2014, Fauchald et al. 2017).

The Arctic and Boreal ecosystems are experiencing climate change effects at a faster rate than anywhere else in the world (Chapin et al. 2000, Ernakovich et al. 2014, Fauchald et al. 2017). Some possible consequences of climate change in these areas include shifts in plant type and production, increased ambient temperature, decreased water availability, and changes to snow pack and melt-off timing (Bavay et al. 2013, Ernakovich et al. 2014, Mod and Luoto 2016). These climate-mediated effects have been shown to have both positive and negative implications for barren-ground caribou herds, affecting their movements and population sizes (Fauchald et al. 2017, Rickbeil et al. 2018). As the landscape in northern latitudes continues to change, it will be important to continue monitoring indices of caribou herd growth or decline

such as calving events and parturition rates (proportion of females who gave birth) to increase understanding of how herds are responding to change.

The Fortymile caribou herd (FCH) is a barren-ground herd that occupies parts of eastern Alaska and western Yukon Territory and is one of the most economically important herds in Alaska for both consumptive and non-consumptive uses (Magoun et al. 2003). This herd has shown dramatic changes in population size and distribution since population size estimates began in the 1920s (Murie 1935, Skoog 1956, Valkenburg et al. 1994, Boertje and Gardner 2000). The FCH has a shorter annual migration than other barren-ground herds such as the Western Arctic herd (WAH) and Porcupine caribou herd (PCH) (Hemming 1971). However, similar to these migratory barren-ground herds and in contrast with non-migratory woodland caribou, females in the FCH migrate to the calving grounds for a pulse calving event in which they give birth within a short window of time (Valkenburg and Davis 1986). During calving, aerial surveys are flown to gather data on parturition rate, calving location and date, and calf survival. These data can provide information about herd dynamics that may be related to habitat conditions on both their summer and winter ranges.

Body condition of a female at different times of year plays a significant role in her reproductive success. Female pre-rut body condition during summer and fall is a major factor in timing of ovulation and subsequently helps explain calving timing the following spring (Cameron et al. 1993). Autumn body condition of a female is closely related to a female's ability to become pregnant (Cameron et al. 1993) which can subsequently affect parturition rate. Poor forage availability on winter ranges can also reduce female body condition, decreasing fetal development and can result in low birth masses and reduced survival rates of neonates (Skogland 1983, Roffe 1993). Calving timing is important because calves born near the median calving date

(the date when 50% of calves have been born) have a higher chance of survival relative to those born before or after the median calving date (Whitten et al. 1992, Griffith et al. 2002). In addition, forage quantity and predation risk affect calf survival on the calving ground (Griffith et al. 2002). With the potential for warmer and wetter summers and winters, increased icing events, increased insect harassment, and changes in dominant vegetation, the quality and quantity of forage can change and energy demands could change (Toupin et al. 1996, Albon et al. 2017). Therefore, the ability to consistently gather data and monitor trends in parturition and calving timing/location can give insight into how the FCH is responding to changes.

Historically, aerial surveys have been the most common method used to gather calving metrics for the FCH, but many factors reduce the feasibility of this method. For example, availability of competent pilots and observers and unsafe flying conditions (weather-related) can preclude or limit aerial survey completion. Distribution of caribou can preclude complete surveys when the herd is located far from fuel caches. Additionally, calving dates and locations estimated from aerial surveys may be inaccurate because of movement by the calf/cow pair following calving. It is very rare to observe a calf/cow pair at the exact calving site (identifiable by the calf being unable to stand and/or observation of a placenta), because the calf is able to walk and follow the cow within 1-4 hours after birth (Lent 1966). Lastly, these surveys pose an inherent safety risk to the pilot and observer (Sasse 2003). In response to the issues and limitations of aerial surveys, we evaluated a method (DeMars et al. 2013) to identify parturition events and calving locations remotely using movement rates based on GPS collar locations.

A decrease in movement rates of GPS-collared animals during calving season has been indicative of calving events in large ungulates including moose, elk, and woodland caribou (Dzialak et al. 2011, Nagy 2011, DeMars et al. 2013, Mcculley et al. 2017, Nicholson et al.

2019). DeMars et al. (2013) developed two models (hereafter: the DeMars method) to estimate calving events for non-migratory woodland caribou based on a drop in movement rates of parturient females.

The applicability of the DeMars method for barren-ground caribou may be affected by behavioral differences between woodland and barren-ground caribou. For example, compared to non-migratory woodland caribou, migratory barren-ground caribou have faster movement rates (e.g., ~10 km/ day, barren-ground; Magoun et al. 2003, vs. <1 km/d, woodland; Rettie and Messier 2001) after calving and during the summer season and there is potential for lack of independence in movements among individual barren-ground caribou (DeMars et al. 2013, Bonar et al. 2018, Cameron et al. 2018). Parturient non-migratory woodland caribou tend to move independently of one another into wooded areas to calve (DeMars et al. 2013). Conversely, parturient migratory barren-ground caribou converge together for a pulse calving event, resulting in the possibility that individual movements may be influenced by the group (Hemming 1971, Fancy et al. 1989). Moreover, as both non-parturient and parturient females move to the calving grounds/summer range there is a possibility that they would both demonstrate a similar drop in movement rates once they arrive at the calving grounds. This could cause the DeMars method to incorrectly identify non-parturient barren-ground females as having calved, biasing population parturition rate upward. Depending on how weather (e.g., delayed snow melt) has affected caribou movement, median calving date estimates from the DeMars method could be biased earlier or later if weather caused a parturient female to either pause before the actual calving event or to not pause until after a calving event. In addition, weather could also cause both parturient and non-parturient females to slow their movement, possibly low enough to imitate a calving event, creating positive bias in the parturition estimate.

Previous applications of the DeMars method estimated individual calving events with 0.77-0.81 agreement with aerial survey for the WAH (Cameron et al. 2018). However, Cameron et al. (2018) noted that the lack of fine-scale temporal resolution in the GPS locations from the collars (8 h fix rate) and a lack of daily visual aerial observations likely reduced their accuracy (Cameron et al. 2018). This method was also tested on the PCH which used fine-scale GPS fix rates (2.5 h) and had more frequent daily observations in the aerial surveys than Cameron et al. (2013) (Chapter 1).

In this study, we broadened the applicability of the DeMars methods by applying them to a barren-ground herd with shorter seasonal migrations and lower annual movement rates than have been tested before. We hypothesized that parturition rates as estimated by aerial survey can be estimated by DeMars methods with negligible bias and sufficient accuracy to be used for management purposes when aerial surveys cannot be flown. The objective of this paper was to compare GPS collar-based estimates of population parturition rates, individual calving events, calving locations, calving dates, and median calving dates obtained from the DeMars et al. (2013) methods to estimates derived from independent visual aerial surveys of the FCH during 2016, 2017 and 2018.

2.3 Methods

Study Area

The calving grounds of the Fortymile caribou herd are located in mountainous east-central Alaska (Figure 2.1). The area encompasses approximately 14,000 km^2 of upland tundra and boreal forest between the Tanana and Yukon rivers in Alaska (Boertje and Gardner 2000). Temperatures in this subarctic/continental climate average -20°C during the long winters and

15°C in the short summers, with average annual precipitation of approximately 30 cm (Climate-Data.org, Valkenburg et al. 1994). Vegetation at lower elevations largely consists of black spruce (*Picea mariana*), and white spruce (*Picea glauca*) with a moss and lichen understory. Upper elevations are dominated by subalpine vegetation primarily dwarf birch (Betula nana) and willow (Salix spp.) (Skoog 1956, Boertje et al. 2017).

Study Population

The FCH is a barren-ground caribou herd that resides in east-central Alaska and adjacent Yukon Territory (Figure 2.1) (Hemming 1971). The population may have been quite large during the 1920's (Murie 1935, Boertje et al. 2012), but by 1973 estimated herd size was only 6,500 (Boertje and Gardner 2000) and by 2017, had increased steadily to 83,000 (Harvest Management Coalition 2019). The primary annual range of the FCH is approximately 77,000 km^2 and the area appears to be positively correlated with population size (i.e., as the population grows or declines so does the size of their range) (Alaska Department of Fish and Game, personal communications, Valkenburg and Davis 1986, Boertje et al. 2012) (Figure 2.1) but the exact nature of this relationship and it's upper limit is not fully understood. The herd is most dispersed in winter, using mainly spruce-dominated forest on ridges and valleys on the edges of the calving ground extending both to the southeast in the Yukon and to the northwest in the White Mountains in Alaska (Valkenburg et al. 1994) (Figure 2.1). The herd moves to the calving ground, comprised of higher elevation alpine tundra in the central part of their annual range in April and May (Valkenburg and Davis 1986, Valkenburg et al. 1994) (Figure 2.1). Peak of calving takes place in mid-May, followed by insect avoidance through June and July.

Aerial Surveys

Aerial surveys were flown in 2016, 2017 and 2018 to estimate parturition status and calving locations and dates of female GPS/VHF collared caribou ≥ 3 years old (n = 50, 49, 46, respectively). The females were collared when they were ≥ 1 year old with Lotek™ collars that had auxiliary VHF transmitters. The collars collected a GPS point every 2.5 hours throughout the study period. Surveys were flown in Piper PA-18™ Super Cub aircraft beginning mid-May through early June with the pilot making observations. Each collared female was located using VHF radio telemetry, nominally every day, and classified as parturient by the presence of antlers and/or distended udder, or a calf at heel (Whitten 1995). The first observation of a cow with a calf was assumed to be the calving location and date and the coordinates were marked with a GPS unit mounted in the aircraft.

Data Management

To prepare the data for application of the DeMars methods, the step length (m) (straight line distance between GPS locations) between each 2.5 hour fix was calculated for every female. Every female's step lengths started with the same time stamp (May 11th, 4:30 AM each year) and followed the same 2.5 hour interval through the end of the calving analysis window (June 10; 296 total possible fixes per female). If a female's GPS collar failed to obtain a location at a specific date/time, that location and the subsequent location were assigned null values. For years 2016-2018, there were 240, 219, and 319 missing fixes across all females and an average of 290, 294, and 290 useable fixes per female, respectively.

Population-based Method (PBM)

DeMars Approach

We initially used the original cumulative distribution function (CDF) method described by DeMars et al. (2013) in conjunction with the bootstrapping modification from Cameron et al. (2018) to identify a calving threshold. A movement rate (m/h) averaged over 3 days post-calving was collected from females with a well-defined calving date and a calf that survived for at least one week (n = 13 out of 50, 25 out of 49, and 16 out of 46 for 2016-2018, respectively). The total number of cows with well-defined calving dates were reduced by 1, 4, and 4 for 2016-2018, respectively, as a result of calf death within one week. A well-defined calving date was taken from a visual observation of a female with a calf on back-to-back observation days in the aerial survey. The beginning of the 3-day movement rate estimate started with the lowest observed movement rate between the last survey observation without a calf to the first observation with a calf from aerial survey.

The distribution of 3-day average movement rates were smoothed by calculating a kernel density estimate. The smoothed distribution was then converted to a cumulative distribution function (CDF) to represent the proportion of the population expected to move at or below a given rate. For this initial run on each individual year, the 3-day average movement rate corresponding to the 98^{th} percentile was interpreted as the calving threshold, in concordance with Cameron et al. (2018). The 98% quantile removes the top 2% of the fastest movement rates and gives the proportion of individuals at or below the corresponding 3-day average movement rate. In their (Cameron et al. 2018) study, the original 99.9% quantile (DeMars et al. 2013) would not allow the model to run correctly possibly due to higher movement rates in the Western Arctic herd (Cameron et al. (2013) compared to woodland caribou in DeMars et al. (2013).

Additionally, to account for variance in movement rates at calving that could influence the population calving threshold, we ran a 1000-iteration bootstrap (with replacement) that sampled 10 of the females with well-defined calving dates each year (n = 13, 25, and 16 for 2016-2018, respectively) and generated a calving threshold for each subset (Cameron et al. 2018). These estimates were combined into a histogram, a kernel density estimate was applied to the histogram, and the maximum kernel estimate was used to identify the most common calving threshold movement rate (Figure 2.2).

We then compiled all adult (≥ 3-yr) female movement rates, parturient and barren, from May 11 to June 10 (n = 50, 49, 46; for 2016-2018, respectively). This calving period was chosen because the earliest recorded calving event for the FCH was May 11th and no calving events have been recorded past June 10th (Alaska Department of Fish and Game, personal communication, Hemming 1971). We used a 3-day moving window to calculate an average movement rate for each 3-day period for every GPS-collared female during the calving period. These 3-day average movement rates were compared to the bootstrapped calving threshold rate found for each year. If a female's 3-day average movement rate fell below the calving threshold, a calving event was declared. The calving event was defined as the date and time of the first GPS fix within the 3-day calving window that the movement rate fell below the threshold.

Using the DeMars et al. (2013) method with the Cameron et al. (2018) bootstrap modification for threshold identification and testing 1, 2, and 3-day movement window averages for all three years, each of the calving thresholds (114 m/h – 256 m/h) were consistently high enough that every female's movement rate (parturient and barren) fell below the thresholds at least once. We also tested different percent quantiles (99, 95, 90, 85, and 80%) that differed from the 98% quantile reported by Cameron et al. (2018) with the original 3-day movement window

average. Still, none of the thresholds produced (all ≥ 100 m/h) were low enough to classify any female as barren. Although a 1-day movement window average and 100 m/h calving threshold worked for the PCH (Chapter 1), any threshold ≥ 100 m/h, regardless of the movement window, was too high for the FCH. Additionally, similar to Chapter 1, all of the bootstrapped kernel density estimates applied to each day movement window had a bimodal or trimodal distribution instead of an expected unimodal distribution (Example: Figure 2.2).

Modifications to DeMars Approach

Similar to the previous research on the Porcupine Caribou Herd (Chapter 1), the methods used to estimate a calving threshold described in DeMars et al. (2013) and Cameron et al. (2018) were modified to improve classifications of parturient and non-parturient females in the FCH. Because the bootstrap method of Cameron et al. (2018) identified high calving thresholds (114-256 m/h) that resulted in classifying all females as parturient, we tested multiple calving thresholds (50, 35, 30 m/h) that were closer to the minimum movement rates observed for females with a well-defined calving date along with multiple movement window averages (1, 1.5, 2, 2.5 and 3-day windows) for each year (2016-2018, respectively).

Individual-based Method (IBM)

The IBM estimated two movement models for each female based on their individual movement rates during the calving analysis period (May 11- June 10): 1) a break (drop) in movement rate (the female did calve) and 2) no break in movement rate (the female did not calve) (DeMars et al. 2013). For the model of barren females, there is one scale parameter, interpreted as mean step length (m), that is expected to remain constant during the analysis period, meaning there is no drop in movement rates to indicate a calving event. The model of

calving females includes three parameters: 1) the mean step length across the analysis period, 2) the breakpoint in step length indicating calving, and 3) the time for the calf and cow to return to mean step length (DeMars et al. 2013, Appendix S3, ece3785-sup-0001-AppendixS1-S4.docx) .

Two sets of constraints are needed to be defined to run the IBM. First, the minimum number of steps before and after a breakpoint was required. For the FCH, we defined this as 3 days (at 10 steps/d, 3 days = 30 steps). The second constraint was the minimum and maximum time for a cow/calf pair to return to the mean movement rate across the entire analysis period, which we defined as 3 days and 15 days respectively (30 and 150 steps). Both of these constraints were similar to those defined by Cameron et al. (2018) (3 days for the first constraint and 5 and 21 days for the second constraint) and were based on observations of barren-ground caribou calf development from Lent (1964). Cameron et al. (2018) also ran a sensitivity analysis and found that the IBM was robust to changes in these constraints.

The IBM used each female's movement rate for each 2.5 hour interval and applied both of the models (non-calving and calving) with the constraints that we defined. We used the lowest Akaike's Information Criterion (AIC) value to identify the best fitting model (DeMars et al. 2013). If a female's best-fitting model was the calving model, the calving event was characterized as the date and time of the GPS fix that occurred at the calving breakpoint estimated by the IBM (Figure 2.4).

Model Evaluation

For both models, estimates of population parturition rate, individual calving events, calving dates, and calving locations were compared to those rates, events, dates, and locations estimated from the aerial surveys to evaluate the models. We estimated the sensitivity

(proportion of correctly classified parturient females), specificity (proportion of correctly classified non-parturient females) and accuracy (proportion of correctly classified females) for each model. The R code (R Core Team 2015) for these models is detailed in DeMars et al. (2013), Appendices S1 and S3 (ece3785-sup-0001-AppendixS1-S4.docx), and edited by Cameron et al. (2018) in the supplementary materials (https://www.nrcresearchpress.com /doi/suppl/10.1139/cjz-2017-0314#.XaUFxkZKggw). We calculated Cohen's kappa statistic (κ) (Cohen 1960) and the maximum attainable kappa (κ_{max}) (Sim and Wright 2005) to assess the magnitude of agreement between aerial survey and model estimates.

In addition, we conducted a series of two-tailed, paired t-tests ($\alpha = 0.05$) to test average across-year (2016-2018) between-model differences in: 1) the average distance between modeled and aerial survey estimates of individual calving site locations, and 2) model accuracy. We also conducted a two-factor (years and techniques) analysis of variance (ANOVA) without replication to test for differences among modeled and the aerial survey estimates of population parturition rate across years. One-tailed, paired t-tests were conducted to test for a difference in false positive and false negative classification rates across years for each model for the FCH data. A significantly higher false positive than false negative classification rate would support the concept of dependence (DeMars et al. 2013) between parturient and non-parturient female movement rates. All these tests likely had low power to detect relatively small differences as a result of a small ($n = 3$ years) sample size.

2.4 Results

Aerial Survey

Calving occurred in the same general area of eastern Alaska during the three study years. For every year, the surveys had a gap of 4-6 days between the first day of survey observations to the second day. On the first day of surveys (May 11), there were few (0-3) calves born. Therefore, surveys were paused for a few days to conserve flight time. Surveys were then resumed around May 20th, prior to the suspected median calving date when, presumably, more calves were born. In addition, there were 2-3 additional days each year during the survey period when no observations were made due to factors such as weather. In total, each year had 6-7 days throughout the survey period (May 11-June 10) in which there were no observations made, primarily at the extreme beginning and end of calving.

In 2016, of the 50 total females surveyed, 41 were parturient (0.82 parturition rate). Of the parturient females, no calf was observed for 4 females, and 13 of the remaining parturient females had well-defined calving dates (observed one day without a calf and then the subsequent day with a calf) and a calf surviving at least one week and, thus, were used to identify a PBM calving threshold.

In 2017, of the 49 total females surveyed, 47 were parturient (0.96 parturition rate). Of the parturient females, no calf was observed for 1 female and 25 females had a well-defined calving date and a calf surviving at least one week.

In 2018, of the 46 total females surveyed, 33 were parturient (0.72 parturition rate). Of the parturient females, no calf was observed for 3 females and 16 females had a well-defined calving date and a calf surviving at least one week.

Population-based Method Performance

The 2.5 and 3-day movement windows tested for calving threshold development resulted in incorrect classifications of every barren female so they were excluded from further analyses. Additionally, the 2-day movement window when combined with the 30 m/h and 35 m/h thresholds also incorrectly classified the barren females and gave early calving dates for those that did calve. Of the remaining combinations, a 1.5-day movement window and a 35 m/h threshold minimized the number of false parturition classifications across all three years (Table 2.1). Additionally, it had an average positive bias of only 0.01 for population parturition rate compared to aerial survey observations across years (Table 2.1). The results we report in this paper therefore were generated using a 1.5-day average movement window and a 35 m/h calving threshold movement rate (Figure 2.3).

In 2016, the PBM estimated a parturition rate of 0.74, and the aerial survey estimated 0.82 (Table 2.2). The accuracy was 0.86, sensitivity was 0.88 and the specificity was 0.78 (Table 2.3). On average, the PBM estimated calving events about 2 days earlier and 4 km away from the aerial survey (ranges of 11 days earlier to 6 days later and 0.05 km to 41.13 km away) (Figure 2.5). The median calving date for 2016 (5/18/16) was 1 day earlier than that of the calving survey (5/19/16) (calving date ranges of 5/11 to 5/26 and 5/12 to 5/26, respectively) (Table 2.2). Examples of incorrect model estimates of calving dates can be found in Figure 2.6.

In 2017, the PBM estimated a parturition rate of 0.92, while aerial survey estimated 0.96 (Table 2.2). The accuracy was 0.92, sensitivity was 0.94 and the specificity was 0.50 (Table 2.3). On average, the PBM estimated calving events about 1 day earlier and 3.32 km away from the aerial survey (ranges of 10 days earlier to 4 days later and 0.05 km to 57.28 km away) (Figure

2.5). The median calving date for 2017 (5/20/17) was 1 day earlier than that of the calving survey (5/21/17) (calving date ranges of 5/13 to 6/7 and 5/16 to 5/29, respectively) (Table 2.2).

In 2018, the PBM estimated a parturition rate of 0.83 while aerial survey estimated 0.72 (Table 2.2). The accuracy was 0.76, sensitivity was 0.91 and the specificity was 0.38 (Table 2.3). On average, the PBM estimated calving events about 3 days earlier and 8.34 km away from the aerial survey (ranges of 17 days earlier to 2 days later and 0.02 km to 60.43 km away) (Figure 2.5). The median calving date for 2018 (5/22/18) was 3 days earlier than that of the calving survey (5/25/18) (calving date ranges of 5/11 to 5/30 and 5/19 to 5/30, respectively) (Table 2.2).

Within both aerial survey and PBM results there was notable variation among years in population parturition rate (Table 2.2) and individual classification accuracy (Table 2.3). On average across all three years, the PBM had an accuracy of 0.85 and aerial and PBM estimates of population parturition rate were both 0.85. The PBM estimated calving sites to be 5.22 km away (95% CI = 2.72 – 8.30) from, and 2 days earlier (95% CI = 3 days earlier – 1 day earlier) than those estimated by aerial survey. In addition, there was a suggestive, but non-significant, difference between false positive and false negative rates for individual parturition classifications (0.45 vs. 0.09, respectively; $t = 2.72$, $P = 0.11$, df = 2) for PBM.

Individual-based Method Performance

In 2016, the IBM estimated a parturition rate of 0.90 while aerial survey estimated 0.82 (Table 2.2). The accuracy was 0.80, sensitivity was 0.93 and the specificity was 0.22 (Table 2.3). On average, the IBM estimated calving events 0.5 days earlier and 4.15 km away from the aerial survey (ranges of 5 days earlier to 7 days later and 0.02 km to 67.07 km away) (Figure 2.5). The

median calving date for 2016 (5/19/16) was the same as the calving survey (calving date ranges of 5/14 to 6/3 and 5/12 to 5/26, respectively) (Table 2.2).

In 2017, the IBM estimated a parturition rate of 1.0 while aerial survey estimated 0.96 (Table 2.2). The accuracy was 0.96, sensitivity was 1.00 and the specificity was 0.00 due to classifying every female as parturient (Table 2.3 and 2.4). On average, the IBM estimated calving events 1 day later and 3.06 km away from the aerial survey (ranges of 4 days earlier to 10 days later and 0.01 km to 29.45 km away) (Figure 2.5). The median calving date for 2017 (5/22/17) was 1 day later than that of the calving survey (5/21/17) (calving date ranges of 5/14 to 6/7 and 5/16 to 5/29, respectively) (Table 2.2).

In 2018, the IBM estimated a parturition rate of 0.98 while aerial survey estimated 0.72 (Table 2.2). The accuracy was 0.74, sensitivity was 1.00 and the specificity was 0.08 (Table 2.3). On average, the IBM estimated calving events were 0.5 days earlier and 3.85 km away from the aerial survey (ranges of 16 days earlier to 14 days later and 0.02 km to 61.03 km away) (Figure 2.5). The median calving date for 2018 (5/25/18) was on the same day as the calving survey (5/25/18) (calving date ranges of 5/14 to 6/6 and 5/19 to 5/30, respectively) (Table 2.2). Examples of incorrect model estimates of calving dates are found in Figure 2.7.

Within both aerial survey and IBM results there was notable variation among years in population parturition rates (Table 2.2) and individual classification accuracy (Table 2.3). On average across all three years, the IBM had an individual classification accuracy of 0.83. Parturition rate from IBM was always greater than from aerial survey but the average difference of 0.13 between IBM and aerial survey was insignificant ($F = 3.85$, $P = 0.12$, df = 2). Across years on average, the IBM estimated calving sites to be 3.69 km away (95% CI = 3.05 – 4.32) from, and on the same day (95% CI = 1 day earlier – 1 day later) than those estimated by aerial

survey. In addition, there was a significantly higher false positive than false negative rate for parturition classifications (0.90 vs 0.02, respectively; $t = 10.14$, $P = 0.010$, df = 2) for IBM.

Differences Between Models and Aerial Surveys Across Years

There was no significant difference in accuracy (0.85 and 0.83, respectively; $t = 0.46$, $P = 0.69$, df = 2), or average distance of model estimated calving locations from aerial survey calving locations (5.2 and 3.69 km, respectively; $t = 1.03$, $P = 0.41$, df = 2) between the PBM and IBM across years. Nor was there a significant difference among aerial survey, PBM and IBM estimates of parturition rate (0.83, 0.83 and 0.96, respectively; $F = 3.85$, $P = 0.12$, df = 2). However, the notable 0.13 average difference, and consistent direction of differences, between IBM and aerial parturition rate estimates (Table 2.2) suggests that a larger sample of years may identify a significant difference.

False positive and false negative parturition classification rates varied among years between the PBM and IBM (Table 2.5). For the PBM-derived results, there was a notable but non-significant difference in false positive vs. false negative parturition classification rates (0.45 and 0.09, respectively; $t = 2.724$, $P = 0.056$, df = 2). However, for the IBM derived results, false positive rates were significantly greater than false negative rates (0.90 and 0.02, respectively; $t = 10.14$, $P = 0.005$, df = 2). Additionally, there was a higher false positive rate for IBM than PBM (0.74 vs. 0.42, respectively; $t = 3.24$, $P = 0.016$).

Kappa and Maximum Attainable Kappa (κ_{max})

As an index of strength of agreement beyond that expected by chance, the magnitude of the kappa statistics for both the PBM and IBM suggested slight to moderate agreement in 2016 (0.58 and 0.18, respectively), fair to poor agreement in 2017 (0.29 & 0.00, respectively) and

slight to fair agreement in 2018 (0.33 & 0.11, respectively) (range of values for Kappa can be ≤ 0 to 1) (Landis and Koch 1977). In 2018, IBM kappa values were at the maximum values they could attain given the constraints of the marginal totals (κ_{max}) (Sim and Wright 2005) which was likely driven by the small number (2) of known non-parturients in the 2018 dataset and the fact that all females were classified as parturient. Additionally, there was only one instance when kappa was statistically different from zero (PBM in 2016) indicating that this model performed significantly better than chance for this year (Table 2.3). Other than this instance, there were no clear differences between PBM and IBM based on kappa and κ_{max} (Table 2.3).

2.5 Discussion

DeMars et al. (2013) suggested that their methods may not have utility for migratory herds due to potential dependence in travel rates between parturient and non-parturient females that migrate as a herd. The woodland caribou herd that was studied by DeMars et al. (2013) to develop the IBM and PBM is a sedentary herd and does not exhibit any distinct migration pattern (Bergerud 1996, Culling et al. 2006). The majority of movements for sedentary caribou are between different forage patches within lowland plains (Johnson et al. 2002, Culling et al. 2006). During calving, an individual parturient female will spatially segregate herself from others, perhaps as a strategy to avoid predation (Bergerud 1985), and move at an average rate of 15 m/h (Culling et al. 2006, DeMars et al. 2013).

In contrast, the two migratory barren-ground caribou herds and one migratory woodland herd which the DeMars method has been applied to resulted in much higher calving threshold movement rates (137 m/h (Western Arctic herd; Cameron et al. 2018), 100 m/h (Porcupine caribou herd; Chapter 1) and 208 m/h (Bonar et al. (2018)) than the 15 m/h threshold estimated by DeMars et al. (2013). Both migratory barren ground herds exhibit very long annual

movements (up to 5,000 km/y for Porcupine caribou; Fancy et al. 1989; up to 4,400 km/y for Western Arctic; Joly and Cameron 2017), have large annual ranges (363,000 km^2 for Western Arctic; Joly et al. 2009; 201,000 km^2 for Porcupine; Caikoski 2016) and aggregate together for a pulse-calving event (Griffith et al. 2002, Cameron et al. 2018). While the FCH exhibits shorter annual movements (up to 2,700 km/y; the maximum annual sum one GPS location per day, May 11-May 10, 2012-2018, from 226 adult female caribou of the FCH) and a smaller annual range (77,000 km^2; ADFG 2019) than other barren-ground caribou (WAH and PCH) they also aggregate for calving (Valkenburg and Davis 1986).

Anecdotal observations argue against dependence in movement rates between migratory barren-ground caribou individuals. Individuals within groups of the FCH can exhibit erratic behavior compared to those around them (Skoog 1956). Skoog (1956) also observed that some groups and some individuals of females traveled at much higher movement rates relative to those around them. In the WAH, parturient females will often stop to give birth and the rest of the group that they are travelling with will continue on (Lent 1966).

Among-individual dependence in movement rates during calving could result in a predominance of false positive parturition classifications compared to false negatives in migratory herds when using the DeMars et al. (2013) models. We found statistical support for a higher false positive than false negative parturition classification rates for IBM for the FCH (0.90 and 0.02, respectively; $t = 10.13$, $P = 0.010$, df = 2) (Table 2.5) but non-significantly higher false positive than false positive rate for PBM (0.45 vs. 0.09, respectively; $t = 2.72$, $P = 0.056$, df = 2) (Table 2.5). This may have contributed to our reduced accuracy for both PBM and IBM (average of 0.85 and 0.83, respectively) compared to the small sample (n = 24, 12 and 10

females among 3 years) accuracy of 1.00 and 0.97, respectively, obtained by DeMars et al. (2013) for sedentary woodland caribou.

Individual classification accuracy would be most important when addressing animal and/or site-specific attributes of calving. Consensus methods in which results from both the PBM and IBM are used when both models agree, such as those employed by Cameron et al. (2018) may improve individual accuracy but at a cost of substantial reduction in sample size and increased costs resulting from the necessity to collect validation data for PBM.

The mechanisms that might explain a higher false positive rate for IBM than PBM (0.74 vs 0.42, respectively; $t = 3.24$, $P = 0.016$) are obscure. The use of validation data to estimate a calving threshold for the PBM from movement rates of known parturient cows with well-defined calving dates may reduce false positive classifications compared to the IBM. IBM simply identifies a break (decline) in movement rates, regardless of the reason for the break. Breaks in movement rates that may be unrelated to calving (e.g., extended foraging in a patch or extended resting due to inclement weather) may increase false parturition classifications by the IBM compared to the PBM.

For the FCH, we found no significant differences between PBM and IBM performance for calving location or accuracy in individual classification of parturient and barren females. However, there was a non-significant, suggestion that IBM population parturition rates had an average positive bias of 0.13 compared to aerial survey (Table 2.2). This potential bias is likely related to the significantly higher average false positive classification rate for the IBM compared to the PBM.

The PBM calving threshold (35 m/h) for the migratory FCH was substantially lower than the calving threshold used for other migratory barren-ground herds (100m/h for the PCH (Chapter 1), 137m/h for the WAH (Cameron et al. 2018) or 208 m/h for migratory woodland herds (Bonar et al. 2018)) but was similar to the 15 m/h (DeMars et al. 2013) and the 23 m/h (Bonar et al. 2018) thresholds derived for sedentary woodland caribou. PBM calving thresholds are expensive to obtain (require validation data), are widely variable among herds and are not consistently related to migratory or sedentary behavior (Table 2.6). Small differences in calving thresholds and moving average window widths can materially affect accuracy and calving date estimation as we have demonstrated for the FCH (Table 2.1). Thus, expensive validation data is required to estimate calving thresholds for the PBM for any new herd.

Cameron et al. (2018) developed a bootstrap method to address potential variation in calving thresholds used in the PBM within the migratory barren-ground WAH. From this method, they obtained a uni-modal distribution of calving thresholds and used the most frequent value as their estimate of the calving threshold. However, for the other migratory barren-ground herds (PCH (Figure 1.2) and FCH (Figure 2.2)) we found multi-modal calving thresholds using the Cameron et al. (2018) bootstrap method. These multiple modes suggest that some migratory barren-ground caribou herds may consist of multiple 'types' of females that naturally move at different average rates during the calving season. Multiple calving thresholds within a herd may reduce accuracy, which may require alternative threshold estimation methods quite different from both the CDF component of DeMars et al. (2013) PBM model and from the Cameron et al. (2018) bootstrap method in order to obtain useable results. We would expect that multi-modal calving thresholds may challenge the accuracy of the PBM in other migratory herds.

There are several important operational considerations for each method. To run the PBM, validation data is required to identify caribou that calved and their calving date in order to estimate a minimum movement threshold for parturient animals. It is necessary to have a training sample of parturient females with a reliable calving status and calving date estimate to develop the calving threshold regardless the method used to estimate the calving threshold (CDF (DeMars et al. (2013), bootstrap and CDF (Cameron et al. (2018), visual estimation (Chapter 1) or matrix method (this study)). The process can very time intensive for the visual and matrix methods. Additionally, although DeMars et al. (2013) showed that the PBM parturition estimates of sedentary woodland caribou were robust to changes in the calving threshold, we tested thresholds that differed by only 5 m/h for migratory barren-ground caribou and total false classifications and parturition rate bias across years varied with each adjustment for the FCH (Table 2.1). Conversely, the IBM can be run with constraint definitions (e.g. time it takes for a calf/cow pair to return to movement rates before the calving event) that can likely be found in literature and Cameron et al. (2018) found that the IBM was robust to changes in these constraints.

There are a few methodological issues that could be addressed in future research. For example, one way to reduce false positive classifications of barren females for the IBM might be to apply a smoothing method similar to that used for the PBM. This could allow for the detection of larger pauses in movement instead of smaller ones possibly related to grazing or resting. For the PBM, future work might develop a method for accommodating multiple calving thresholds, taking into consideration that there might be different types of animals that move at different speeds at calving (i.e., understanding the multi-modal distribution of calving thresholds resulting from the Cameron et al. (2018) bootstrap method). Future studies could also apply the method

described by Cameron et al. (2018), in which results from both the PBM and IBM are used when both models agree. This consensus method may give higher accuracy than only using one method as was found in their study, but at the cost of an approximate 25-30% reduction in effective sample size (Cameron et al. 2018) and greatly increased expense due to the validation data requirement for the PBM. Including other movement analyses such as turning angles, minimum convex polygons, and behavioral change point analyses, which have been used to identify calving events in other large ungulates, may also increase the accuracy of detection of calving events (Mcculley et al. 2017, Nicholson et al. 2019). Lastly, simulation studies need to be conducted to estimate whether the average individual accuracy estimates (0.85 and 0.83 for PBM and IBM, respectively) materially affect population projections.

2.6 Management Implications

Location and timing of calving and parturition rate can all be important indicators of habitat quality, forage availability, and predictors of future population growth or decline (Cameron et al. 1993, Griffith et al. 2002, Couturier et al. 2009). The method developed by DeMars et al. (2013) provides an alternative way to monitor calving if aerial surveys cannot be conducted due to weather, personnel, equipment or fiscal constraints. For wide ranging migratory animals, the primary advantage of GPS movement rate methods is that there is complete coverage of a species annual range. This allows for a more complete assessment of calving status of all GPS collared individuals in a herd, when weather or fuel availability precludes access to all animals, and can identify major shifts in calving that might be missed from aerial survey alone.

If calving surveys cannot be conducted, the PBM performed no worse than the IBM for the FCH, 2016-2018. Comparing PBM to IBM, respectively hereafter, the PBM gave: 1) average

individual accuracy not significantly different from IBM (0.85 vs. 0.83; $t = 0.46$, $P = 0.69$, df = 2) and 2) annual average distance between aerial survey and model calving locations not significantly different from IBM (5.2 vs 3.7km, $t = 1.03$, $P = 0.41$, df = 2). In addition, population parturition rates estimated by the PBM, IBM, and aerial surveys were not significantly different (0.83, 0.96, 0.83, respectively; $F = 3.85$, $P = 0.12$, df = 2). Where the DeMars models differed was in estimates of false positive classification rates. The IBM had a significantly higher false positive rate than PBM (0.74 vs. 0.42, respectively; t = -3.24, P = 0.032, df = 2) which likely contributed to the notable, but not significantly different, population parturition rate estimate for IBM compared to aerial survey (0.96 vs. 0.83, respectively; $F = 3.85$, $P = 0.12$, df = 2).

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2.9 Figures

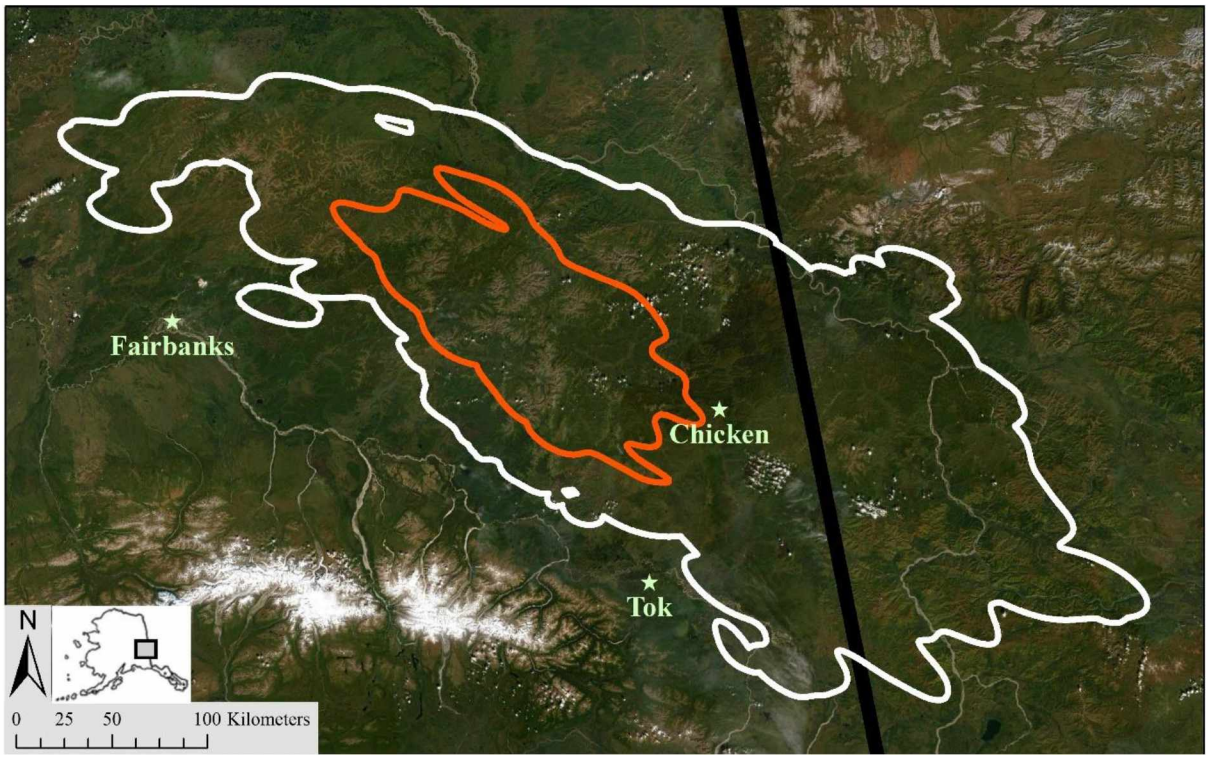

Figure 2.1: Fortymile herd annual range and extent of calving map. Annual range of the Fortymile caribou herd (white line) from October 2015 – September 2018 and extent of calving (orange line) for 2016-2018 (Alaska Department of Fish and Game, personal communication).

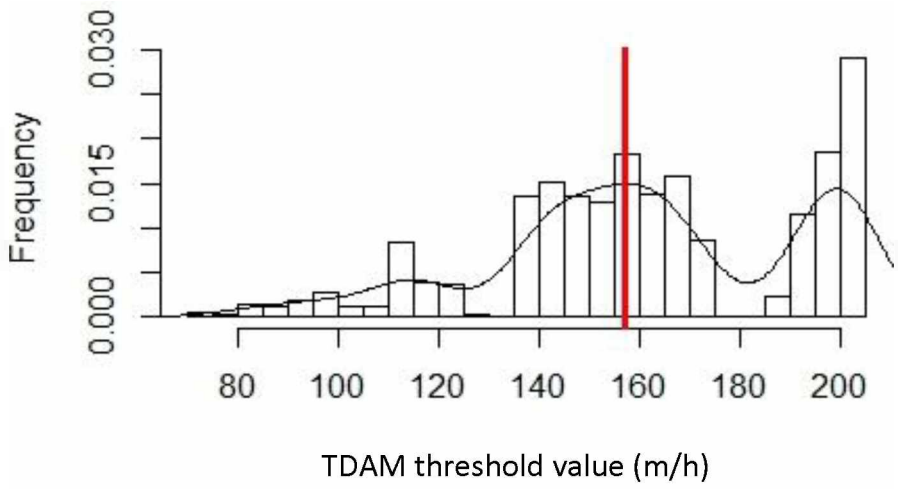

Figure 2.2: Calving threshold bootstrap histogram example. A histogram showing an example distribution of frequencies of calving threshold 3-day average movement rates (TDAM)(m/h) found for females with a well-defined calving date from 2017 (n = 25) given from a 1,000-iteration bootstrap that sampled 10 individuals at a time (with replacement). A kernel density estimate was applied to the histogram (black line) and the maximum of the kernel density estimate (red vertical line) represented the most common three-day average movement rate and this was used as the calving threshold (red line) (157 m/h).

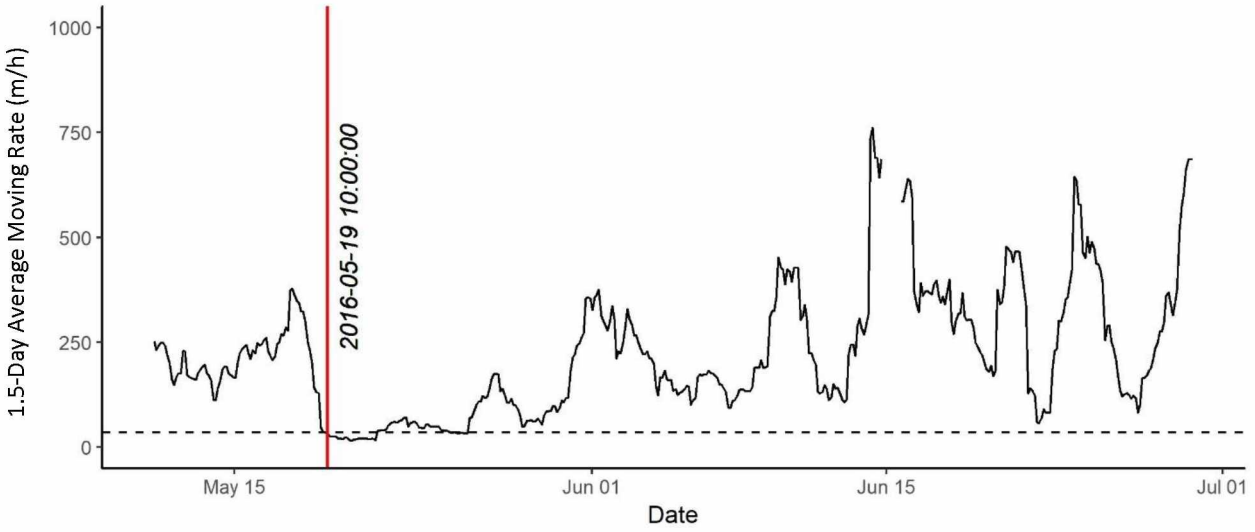

Figure 2.3: Population-based method output. Population-based method parturition estimate for a Fortymile caribou herd female in 2016. The calving date (red vertical line) estimate was May 19, 2016 with 1.5 average movement window (solid black line) and 35 m/h calving threshold (horizontal dashed line) rate.

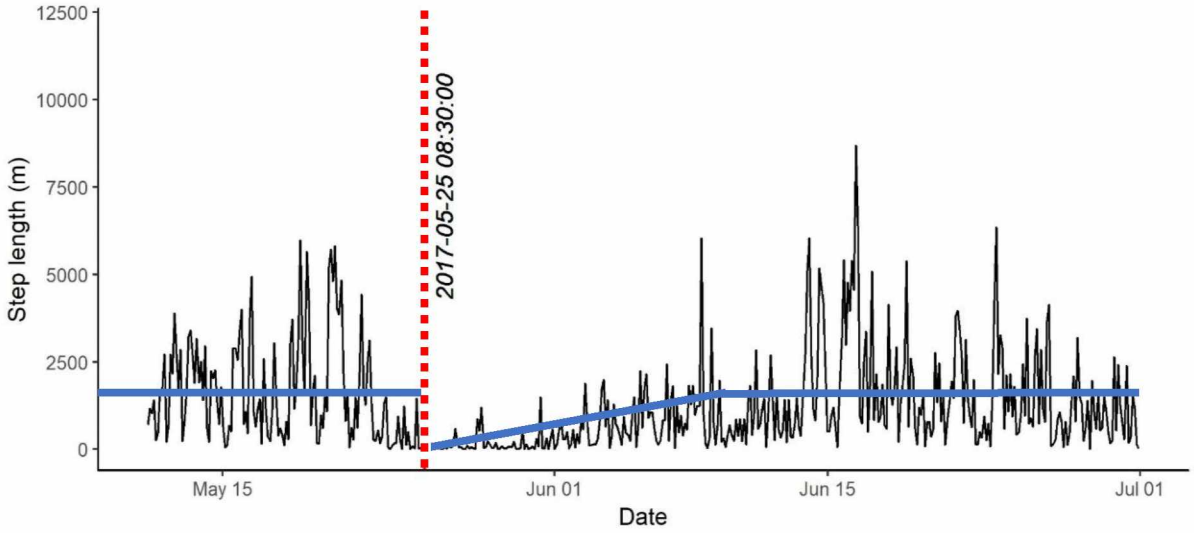

Figure 2.4: Individual-based method output. Individual-based model parturition estimate for a Fortymile caribou herd female in 2017. The calving date (red dashed vertical line) estimate was May 25, 2017, with parameters set at 30 steps before and after a breakpoint, and a max and min of 150 and 30 steps, respectively for a cow/calf pair to return to pre-average movement rates.

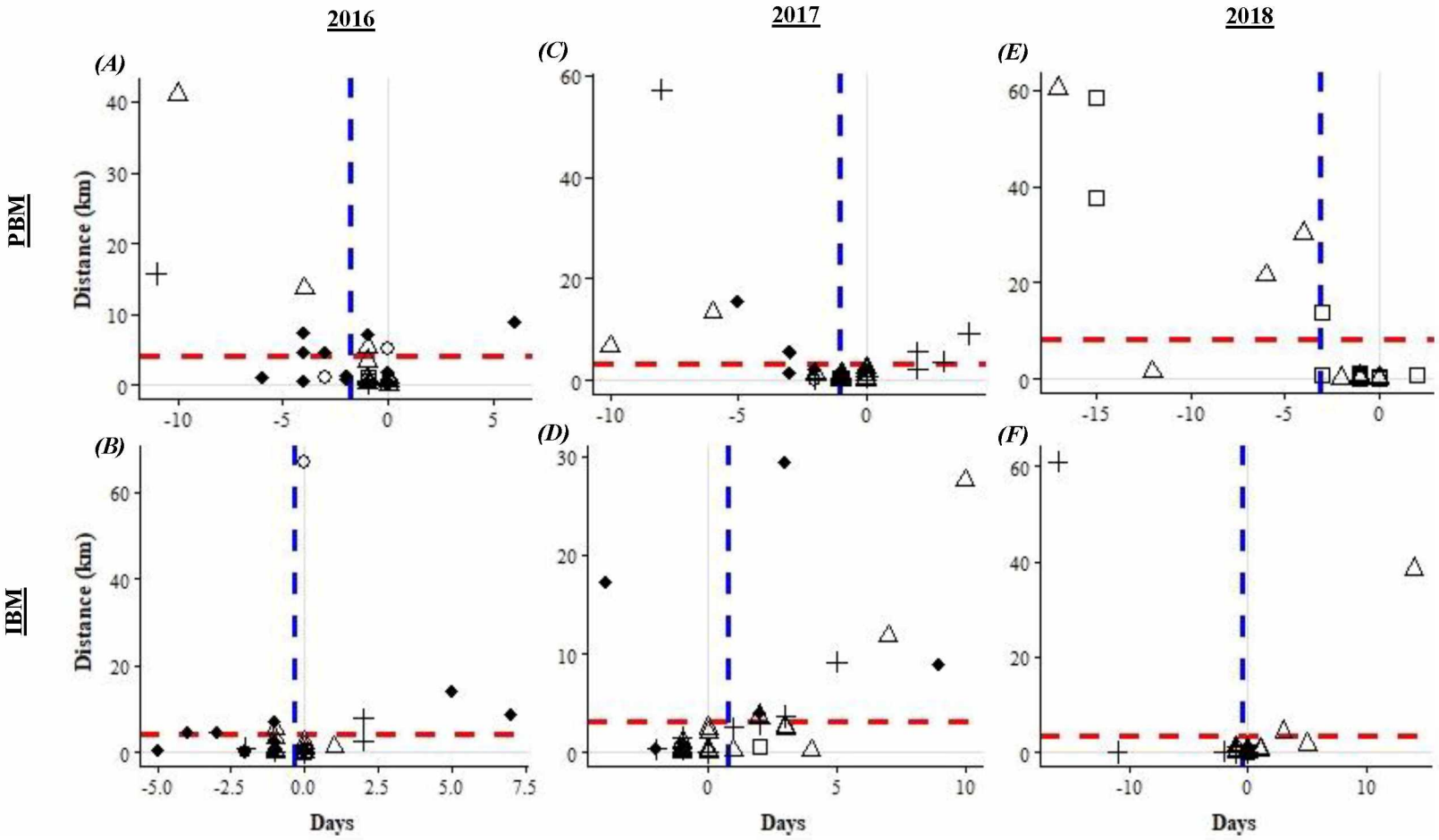

Figure 2.5: Distance and days between estimates of calving date and location for 2016-2018. Distance and number of days between population-based method (PBM) or individual-based method (IBM) estimated calving sites and aerial survey estimates for the Fortymile caribou herd (FCH) for 2016-2018. Along the y-axis is distance (km) from the calving sites observed in aerial surveys in 2016 (A, B), 2017 (C, D), and 2018 (E, F) to the calving site estimated by (A, C, E) the PBM and (B, D, F) the IBM. The red horizontal dashed line represents the average distance (km). Along the x-axis is the number of days before or after the aerial observed calving date in 2016 (A, B), 2017 (C, D), and 2018 (E, F) to the calving site estimated by (A, C, E) the PBM and (B, D, F) the IBM (negative implying earlier than the aerial survey observations, positive implying later than aerial survey observations). The blue vertical dashed line represents the average time difference for each model. The shape of the symbols represents the number of days between observations during aerial surveys, 0 days means the first time the female was observed she had a calf at heel, 1 day means she was seen on initial observation without a calf and the following day with a calf, 2 days means she was seen the first day without a calf, there was no observation the second day, and she was seen with a calf on the third day, etc.

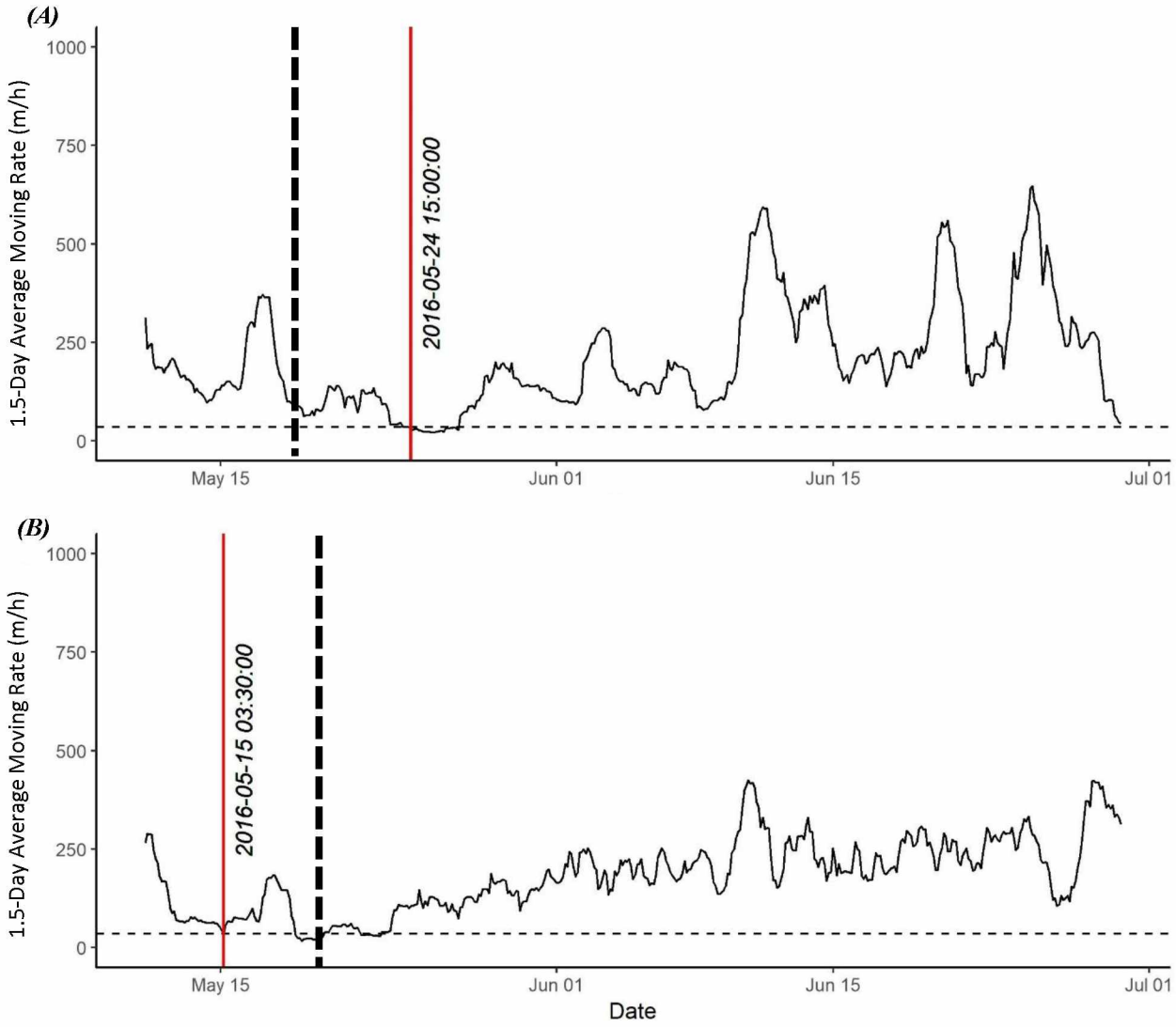

Figure 2.6: Examples of population-based method incorrect calving date estimates. Examples of the population-based method (PBM) incorrectly identifying a calving date, based on their movement rate (solid black line) declining below the calving threshold (horizontal black dashed line) for two females in the Fortymile caribou herd in 2016. (A) The model estimated calving date (red solid vertical line) was May 24th, 2016, the observed calving date from the aerial survey (black dashed vertical line) was May 18th, 2016. (B) The model estimated calving date (red solid vertical line) was May 15th, 2016, the observed calving date from the aerial survey (black dashed vertical line) was May 19th, 2016, this female was seen on May 18th without a calf.

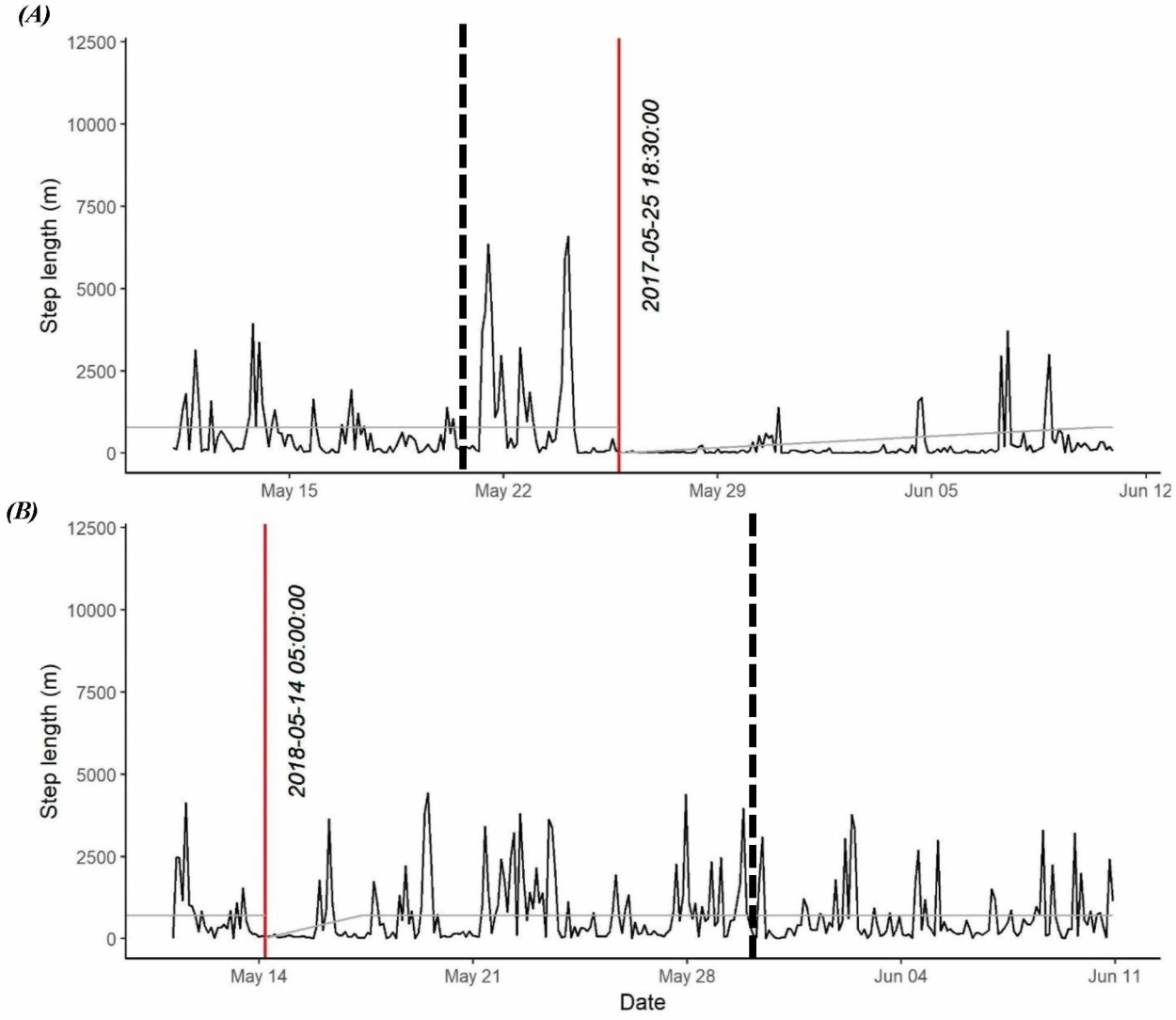

Figure 2.7: Examples of individual-based method incorrect calving date estimates . Examples of the individual-based method incorrectly identifying a calving date for two females in the Fortymile caribou herd in 2017 and 2018. (A) The model estimated calving date (red solid vertical line) was May 25th, 2017, the observed calving date from the aerial survey (black dashed vertical line) was May 20th, 2017. (B) The model estimated calving date (red solid vertical line) was May 14th, 2018, the observed calving date from the aerial survey (black dashed vertical line) was May 30th, 2018, this female was seen on May 28th without a calf.

2.10 Tables

Table 2.1: 'Matrix' method for calving threshold determination . The total false classifications (both false positives and false negatives) of females and average parturition rate bias across 2016, 2017 and 2018 for different calving thresholds and movement window average combinations for testing the Population-based method (PBM) on the Fortymile caribou herd (FCH). In this table, we only present the combinations that yielded the most accurate classifications of parturient or not. The 35 m/h threshold and 1.5-day movement average is outlined as it minimized total false classifications and parturition rate bias and was

Calving Thresholds	**30 m/h**		**35 m/h**		**50 m/h**		
Movement Window Average	1 Day	1.5 Day	1 Day	1.5 Day	1 Day	1.5 Day	2 Day
Total False Classifications	25	23	24	20	24	24	27
Average Parturition Rate Bias	9%	-5%	13%	1%	17%	9%	5%

Table 2.2: Parturition rate and median calving date estimates. The parturition rate (percent of parturient females) and median calving date (date in which 50% of calves have been born) estimated from population-based method (PBM) and individual-based method (IBM) outputs compared to that estimated from the aerial survey for 2016, 2017 and 2018.

	Method	Parturition Rate	Median Calving Date
2016	Survey	82%	5/19/2016
	PBM	74%	5/18/2016
	IBM	90%	5/19/2016
2017	Survey	96%	5/21/2017
	PBM	92%	5/20/2017
	IBM	100%	5/22/2017
2018	Survey	72%	5/25/2018
	PBM	83%	5/22/2018
	IBM	98%	5/25/2018
Average	Survey	83%	
	PBM	83%	
	IBM	96%	
Standard Deviation	Survey	12%	
	PBM	9%	
	IBM	5%	

Table 2.3: Sensitivity, specificity, accuracy, kappa, and κ_{max} estimates for both models. Measures of sensitivity (proportion of correctly classified parturient females), specificity (proportion of correctly classified non-parturient females), and accuracy (proportion of correctly classified females) of the population-based method (PBM) and individual-based method (IBM) in estimating parturition classifications of female caribou found in aerial surveys. Additionally, the reported kappa (κ) statistic and maximum attainable kappa (κ_{max}) found for each model with the 95% confidence intervals parenthetically listed below each kappa statistic. The PBM was run at the 1.5day35m calving threshold. The IBM was run with the parameters identified in the methods: 3 days allowed before and after a breakpoint, maximum time for calf/cow pair to return average movement rate of 15 days, and minimum time for calf-cow pair to return average movement rate of 3 days (step lengths: 30, 150, 30 respectively).

Performance Measure	Year	PBM	IBM
Sensitivity	2016 (*n = 41*)	0.88	0.93
	2017 *(n = 47)*	0.94	1.00
	2018 *(n = 33)*	0.91	1.00
	Average	0.91	0.98
	Standard Deviation	0.03	0.04
Specificity	2016 *(n = 9)*	0.78	0.22
	2017 *(n = 2)*	0.50	0.00
	2018 *(n = 13)*	0.38	0.08
	Average	0.55	0.10
	Standard Deviation	0.21	0.11
Accuracy	2016 *(n = 50)*	0.86	0.80
	2017 *(n = 49)*	0.92	0.96
	2018 *(n = 46)*	0.76	0.74
	Average	0.85	0.83
	Standard Deviation	0.08	0.11
Kappa (κ)	2016	0.58 (0.29 - 0.87)	0.18 (-0.27 – 0.63)
	2017	0.29 (-0.37 - 0.96)	0.00
	2018	0.33 (-0.01 - 0.68)	0.11 (-0.33 - 0.54)
κ_{max}	2016	0.82	0.67
	2017	0.64	0.00
	2018	0.70	0.11

Table 2.4: Confusion matrices from aerial survey data. Confusion matrices of the raw data collected from the 2016, 2017 and 2018 aerial surveys compared to the output of the population-based method (PBM) and individual-based method (IBM). 'Yes' means the female was classified as parturient. 'No' means the

(A)

2016

		Survey		
		Yes	No	Total
PBM	Yes	36	2	38
	No	5	7	12
	Total	41	9	50

		Survey		
		Yes	No	Total
IBM	Yes	38	7	41
	No	3	2	9
	Total	41	9	50

(B)

2017

		Survey		
		Yes	No	Total
PBM	Yes	44	1	45
	No	3	1	4
	Total	47	2	49

		Survey		
		Yes	No	Total
IBM	Yes	47	2	49
	No	0	0	0
	Total	47	2	49

(C)

2018

		Survey		
		Yes	No	Total
PBM	Yes	30	8	38
	No	3	5	8
	Total	33	13	46

		Survey		
		Yes	No	Total
IBM	Yes	33	12	45
	No	0	1	1
	Total	33	13	46

Table 2.5: Proportion of false positives and false negatives for both methods. Proportion of false positive and false negative parturition classification from the population-based method (PBM) and the individual-based method (IBM) for the Fortymile caribou herd (FCH) and the average proportion and standard deviation of false positives and negatives across years, herds and models.

	PBM		IBM	
	False Positives	False Negatives	False Positives	False Negatives
2016	0.22	0.12	0.78	0.07
2017	0.50	0.06	1.00	0.00
2018	0.62	0.09	0.92	0.00
Average	0.45	0.09	0.90	0.02
Standard Deviation	0.21	0.03	0.11	0.04

Table 2.6: Summary of other studies that have implemented the DeMars methods. Calving thresholds (m/h), movement window averages (days), GPS collar fix rates (hours), geographic location, and model accuracy for the different types of caribou herds (woodland or barren-ground) and the different types of migration (migratory or sedentary) from other studies and this study that implemented the population-based method

	Type of Herd	Name of Herd	Geographic Location	Calving Threshold (m/h)	Movement Window Average (Days)	GPS Collar Fix Rates (Hours)	Accuracy	
							PBM	IBM
Sedentary	Woodland	4 Different Boreal Herds[1]	British Columbia	15	3	2	1.00	0.97
		Fogo Island[2]	Newfoundland	23	3	2	0.89	0.56
	Woodland	Middle Ridge[2]	Newfoundland	208	3	2	1.00	0.40
Migratory	Barren-ground	Fortymile	Alaska	35	1.5	2.5	0.85	0.83
		Porcupine[3]	Alaska	100	1	2.5	0.85	0.88
		Western Arctic[4]	Alaska	137	3	8	0.81	0.77

[1] DeMars, C. A., M. Auger-Méthé, U. E. Schlägel, and S. Boutin. 2013. Inferring parturition and neonate survival from movement patterns of female ungulates: A case study using woodland caribou. Ecology and Evolution 3:4149–4160.

[2] Bonar, M., E. Hance Ellington, K. P. Lewis, and E. Vander Wal. 2018. Implementing a novel movement-based approach to inferring parturition and neonate caribou calf survival. PLoS ONE 13:1–16.

[3] Chapter 1

[4] Cameron, M., K. Joly, G. A. Breed, L. S. Parrett, and K. Kielland. 2018. Movement-based methods to infer parturition events in migratory ungulates. Canadian Journal of Zoology 1–37.

General Conclusion

Location and timing of calving and parturition rate are all important indicators of habitat quality, forage availability, and may be predictors of future population growth or decline (Cameron et al. 1993, Griffith et al. 2002, Couturier et al. 2009). The methods developed by DeMars et al. (2013) provide an alternative way to monitor calving if aerial surveys cannot be conducted due to weather, personnel, equipment or fiscal constraints. For wide ranging migratory animals, the primary advantage of GPS movement rate methods is that there is complete coverage of a species annual range. This allows for a more complete assessment of calving status of all GPS collared individuals in a herd in years when weather or fuel availability precludes access to all animals, and can identify major shifts in calving that might be missed during these incomplete years.

More years of data would be required for additional statistical power but for both the PCH and FCH, I found no significant difference between PBM and IBM in: 1) individual classification rate accuracy (0.85 vs. 0.88, respectively; $t = -7$, $P = 0.09$, df = 1 and 0.85 vs. 0.83, respectively; $t = 0.46$, $P = 0.69$, df = 2) or 2) annual average distance from aerial survey calving locations (8.9 vs. 7.8 km, respectively; $t = 0.16$, $P = 0.90$, and 5.2 vs. 3.7 km, respectively; $t = 1.03$, $P = 0.20$). Median date of calving was estimated within 0-3 days of that estimated by aerial survey for both PBM and IBM. Additionally, population parturition rate estimates from aerial survey, PBM and IBM were not significantly different for the PCH or FCH (0.91, 0.88 and 0.95, respectively; $F = 0.67$, $P = 0.60$, df = 2, and 0.83, 0.83 and 0.96, respectively; $F = 3.85$, $P = 0.12$, df = 2). Although not statistically significant, the IBM parturition rate did have a consistent average positive bias for the FCH (0.13, Table 2.2) as well as a slight average positive bias for

the PCH (0.04, Table 1.1). These suspected differences might be supported or rejected with additional years of data.

DeMars et al. (2013) posed a potential issue of lack of independence when applying their models to migrating caribou that aggregate at calving. They surmised that the movements of a parturient female could affect the movements of non-parturient females, and could lead to misclassifying non-parturient females as parturient because non-parturient females might slow down when nearby parturient females stop to calve. For the FCH, we found statistical support for a higher false positive than false negative parturition classification rate for IBM (0.90 and 0.02, respectively; $t = 10.13$, $P = 0.010$, df = 2, Table 5) and a notable but non-significant higher false positive than false negative rate for PBM (0.45 vs. 0.09, respectively; $t = 2.72$, $P = 0.056$, df = 2). Similarly, there was a notable but non-significant tendency toward a higher false positive than false negative rate for both the PBM and IBM for the PCH (0.50 vs. 0.05 for IBM, respectively; $t = 0.92$, $P = 0.26$, df=1; 0.38 vs. 0.11 for PBM, respectively; $t = 0.80$, $P = 0.29$, df = 1). The false positives may have contributed to our reduced accuracy for both PBM and IBM for both herds (FCH cross-year averages of 0.85 and 0.83, respectively; PCH cross-year averages of 0.85 and 0.88, respectively) compared to the small sample (n = 24, 12 and 10 females among 3 years) accuracy of 1.00 and 0.97, respectively, obtained by DeMars et al. (2013) for sedentary woodland caribou.

Across all herds that the PBM has been applied to, migratory and sedentary, there has been a wide range (15 – 208 m/h) in PBM calving thresholds (Table 2.6). PBM calving thresholds are expensive to obtain (require validation data), are widely variable among herds and are not consistently related to migratory or sedentary behavior (Table 2.6). Small differences in PBM calving thresholds and moving average window widths can materially affect accuracy and

calving date estimation as we have demonstrated for the FCH (Table 2.1). Thus, expensive validation data would be required to estimate calving thresholds for the PBM for any new herd.

There are a few methodological issues that could be addressed in future research. For example, one way to reduce false positive classifications of barren females for the IBM might be to apply a smoothing method similar to that used for the PBM. This could allow for the detection of larger pauses in movement instead of smaller ones possibly related to grazing or resting. For the PBM, future work might develop a method for accommodating multiple calving thresholds, taking into consideration that there might be different types of animals that move at different speeds at calving (i.e., understanding the multi-modal distribution of calving thresholds resulting from the Cameron et al. (2018) bootstrap method). Future studies could also apply the consensus method described by Cameron et al. (2018), in which results from both the PBM and IBM are used when both models agree. This method may give higher accuracy than only using one method as was found in their study, but at the cost of an approximate 25-30% reduction in effective sample size (Cameron et al. 2018) and greatly increased expense due to the validation data requirement for the PBM. Including other movement analyses such as turning angles, minimum convex polygons, and behavioral change point analyses which have been used to identify calving events in other large ungulates may also increase the accuracy of detection of calving events (Mcculley et al. 2017, Nicholson et al. 2019). Lastly, simulation studies need to be conducted to estimate whether the average individual accuracy estimates materially affect population projections.

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